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by D.R. Seip

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FORAGING ECOLOGY AND NUTRITION OF STONE'S SHEEP

DALE ROY SEIP[1]

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October 1983

[1] Present address: Forestry Wildlife Group, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia V6T 1W5

ABSTRACT

This study compared the foraging behaviour and nutrition of Stone's sheep (*Ovis dalli stonei*) which had access to burned range to that of sheep on unburned range throughout the year. In winter, sheep were restricted to areas with less than 25-30 cm of snow. Grazing pressure was high on these restricted winter ranges. The poor winter nutrition was reflected in low fecal nitrogen and DAPA levels and high *Protostrongylus* spp. counts. In spring, sheep used either natural or fire-induced subalpine clearings to obtain early new plant growth. Forage quantity was much lower on unburned ranges, but biting rate and foraging time were the same as on burned ranges with high forage biomass. Quality of available forage and food intake were also similar. Sheep moved to higher elevations as the season progressed which provided them with access to the higher quality alpine forage. Regular use of mineral licks in summer apparently satisfied their sodium requirement. Lamb production was low following severe winters, presumably due to poor nutrition. An explanation for changes in lamb production based on density-dependent selective feeding was developed. A model of nutrient intake is developed to investigate the seasonal pattern of nutrition on burned and unburned ranges.

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INTRODUCTION

The concept of an animal population being food limited implies that if the population grows too large, the animals eat most of the food, cannot find enough to eat and starve to death, or forego reproduction. Mountain sheep (Ovis spp.) eat grass. Because there is usually a lot of grass around, it may seem strange to suggest that mountain sheep are food limited. Even on heavily used winter ranges, mountain sheep usually consume only 50 to 80% of the standing crop of grass by the end of the winter (Luckhurst 1973; Stelfox 1976; Hoefs and Brink 1978). Similarly, deer (Odocoileus spp.) are usually surrounded by abundant amounts of browse and moose (Alces alces) never eat the last standing willow shrub.

But we know that sheep and other wild ungulates are nutritionally stressed, particularly in winter. Bighorn sheep (O. canadensis) regularly suffer massive die-offs when overgrazing leads to malnourished sheep (Stelfox 1976). Viable lamb production of mountain sheep is correlated with winter nutrition (Hoefs and Brink 1978; Stelfox 1976) and can be improved by supplemental feeding (Ramsay 1980) or by harvesting ewes to reduce competition (Smith and Wishart 1978). Similar nutritional problems are known for other ungulates (Sinclair 1977; McCullough 1979). Yet in almost all cases of nutritional stress there is still food available.

The problem the animal faces is not simply to obtain enough food but rather to obtain enough food of suitable quality. It is well known that ungulates can die of starvation with a stomach full of low-quality food (Pearson 1969). The animal's efficiency in obtaining a highly nutritious diet will have a major impact on its condition and fitness. Therefore, one would expect that animals will be well adapted to forage efficiently. The interactions between the range characteristics and the foraging behaviour of a species constitutes the foraging ecology of that species. The optimum foraging behaviour will vary depending on the characteristics of the foraging environment. Animals should alter their foraging behaviour accordingly to optimize their nutritional intake. That is the focus of this thesis.

Range burning is widely used in northern British Columbia in an effort to improve wildlife habitat. Fire converts subalpine spruce and poplar forest into grassland which is often used by Stone's sheep (O. dalli stonei). This alteration of habitat provided an opportunity to

study how Stone's sheep modify their foraging behaviour in response to a change in range characteristics. In addition, I tried to determine the effect of range burning on the nutrition and population dynamics of Stone's sheep populations in order to evaluate the benefits of range burning for the management of Stone's sheep.

STONE'S SHEEP

Mountain sheep in North America are divided into two species, the bighorns (Ovis canadensis) in the south and the thinhorns (Ovis dalli) in the north. The thinhorns are further divided into two subspecies, the all-white Dall's sheep (O.d. dalli) and the dark-bodied Stone's sheep (O.d. stonei). The two subspecies interbreed to produce an intermediate form know as Fannin's sheep in the central Yukon where their ranges meet. Stone's sheep inhabit mountainous areas of northern British Columbia and the southern Yukon. This subspecies has been little studied in the past. Geist (1971) concentrated on the social behaviour of these animals, Luckhurst (1973) conducted a range study, and Elliott (1978) discussed the effect of range burning on horn growth of Stone's sheep. In addition to studying the foraging ecology of these animals, the present study provided an opportunity to learn more about the general ecology of this important big-game animal.

NUTRITION OF RUMINANTS

Stone's sheep are ruminants. An understanding of the foraging ecology of the species is impossible unless one considers both the advantages and the constraints that being a ruminant entails. The major advantage of being a ruminant is the ability to digest hemicellulose and cellulose in plant material that would be largely undigestible for a non-ruminant. In addition, the rumen microflora can manufacture useful proteins from recycled nitrogen wastes and also produce various essential vitamins for the animal (Church 1980).

The limiting factor to the efficiency of the ruminant digestive system is the rate at which food can be processed. The maximum forage intake in ruminants is limited by the passage rate through the gut (Blaxter et al. 1961; Conrad et al. 1964). Passage rate through the gut is relatively constant but declines somewhat when more fibrous forage is consumed (Phillipson and Ash 1965). Because passage rate is relatively constant, the only way that intake can increase is for more of the food to be

digested.

The gross energy content of most forages is relatively constant and averages 4.4 kcal/g (Maynard et al. 1979). How much of this caloric energy is usable by the animal depends on how digestible the forage is because there is a near 1:1 relationship between dry matter digestibility and energy digestibility (Moir 1961).

Because forage digestibility influences both the maximum forage intake and the digestible energy content of that food, changes in digestibility have a multiplicative effect on the animal's energy intake. Therefore, data on the digestibility of forage allow us to make important predictions about the nutrient intake of ruminants.

One objective of this study was to collect forage samples throughout the year for digestibility and protein analyses. Because grazing animals feed selectively, quality analysis of available herbage may not represent the quality of the food that the animal actually eats. It is a very frustrating task to decide what items of the total plant biomass are actually food for Stone's sheep. It is much more satisfactory if one can measure the quality of the food actually selected by the animal. I attempted this by analysing fecal samples for protein and diaminopimelic acid (DAPA) content, two variables which are correlated with the quality of food consumed by a ruminant (Hebert 1973; Nelson et al. 1982). This information describes the seasonal pattern of food quality. Comparison of forage quality, fecal protein, and DAPA levels between burned and unburned ranges provided a test of the hypotheses:

i) Forage quality (digestibility and protein) is superior on burned ranges.

ii) Sheep feeding on burned ranges have a higher quality of food intake than sheep using unburned ranges.

Analysis of mineral concentrations in forage and soils was also conducted in an effort to determine if the sheep encountered any serious mineral deficiencies. Mineral lick behaviour was studied to see how the animals dealt with the problem of mineral nutrition.

FOOD SELECTIVITY

Ungulates selectively feed on those items which are most nutritious for them. This selectivity occurs at several different levels: selection of range, selection of particular plants on that range, and selection of plant parts (Jarman and Sinclair 1979). Ruminants are more efficient at selecting a nutritious diet when free-ranging than when presented with processed rations (Baile and Forbes 1974). This observation indicates that the animals do not detect the nutrient quality directly but rather detect cues which are positively correlated with quality such as low fibre content or new growth versus dead material. Arnold (1966) demonstrated that smell and taste are the most important senses used in selective feeding by sheep.

I examined selective feeding of Stone's sheep by observing seasonal patterns of range use and by comparing food habits with species availability. This information, in conjunction with forage quality data, was used to test the hypothesis:

iii) Stone's sheep select ranges and food items which provide the best nutrition available.

Estimates of food quality based on fecal protein analyses were compared to forage quality to test the hypothesis:

iv) Quality of food eaten is superior to the average quality of available herbage due to selective feeding.

INTAKE RATE

In addition to selecting high quality food, the grazing ungulate must also maintain an adequate intake rate. Presumably there is an inverse relationship between selectivity and intake rate. An animal selecting only high quality items will probably have a lower intake rate than an animal feeding non-selectively, and an animal that is too selective may not be able to obtain enough food. Therefore, the animal should modify its foraging behaviour to achieve the optimum trade-off between these two factors. Optimum foraging theory (Schoener 1971) would predict that:

v) Sheep feed in such a way as to maximize their net energy intake rate.

The optimum strategy will vary with different range conditions and may vary with sex and body size of individuals. Testing this hypothesis requires information on factors influencing the intake rate of sheep.

It may seem logical that intake rate would go up as the quantity of forage increases. However, in grazing domestic sheep, intake rate remains constant over a wide range of plant densities but is greatly influenced by grass tiller length which determines the bite size (Allden and Whittaker 1970).

It is not possible to measure directly the intake rate of free-ranging wild ungulates. Detailed studies of ungulate foraging behaviour will probably have to rely on captive or semi-tame animals. However, there are some components of the foraging behaviour of free-ranging animals that can be measured and which we would expect to be related to intake rate. I recorded biting rate and daily foraging time of sheep under different range types and conditions to test some hypotheses relating to the effect of range characteristics and range burning on intake rate:

vi) Foraging time and biting rate are related to forage quantity and/or grass tiller length.

vii) Foraging time is less and biting rate of sheep is higher on burned range than on unburned range.

The information on foraging rates was integrated with the forage quality data and evaluated in the context of the optimal foraging hypothesis i.e., maximization of net energy intake rate.

POPULATION CONDITION AND POPULATION DYNAMICS

If food limitation of sheep populations does not mean that the animals eat all the food, what does it mean? Heavy selective grazing by sheep can gradually degrade the quality of the remaining forage on the range in a density-dependent manner (Arnold 1960a). The process will be most pronounced during the non-growing season when grazed vegetation is not being replaced by new growth. For mountain sheep at normal population densities, winter is probably the only time when grazing can significantly degrade the available forage quality. In this study, data were collected to test the hypothesis:

viii) Selective grazing by Stone's sheep in winter removes high quality forage and thereby degrades the quality of the range that winter.

Ungulates faced with a progressively deteriorating food source would be forced to select a progressively poorer diet. Below a certain forage digestibility the animal would be unable to compensate by eating more because of gut capacity. The resultant decrease in nutrient intake would be expected to have a negative effect on the growth rates, condition, and population dynamics of the animals.

For Stone's sheep I attempted to test the hypotheses:

ix) Horn and body growth, lamb production, and parasite levels are related to winter nutrition.

x) Horn growth, body growth, and lamb production are greater and parasite levels are lower in sheep using burned range compared to sheep using unburned range.

Dr. Fred Bunnell initiated this project and provided guidance and support throughout. Drs. M. Pitt, J. Kimmins, A. Sinclair, and L. Larson were the other members of my advisory committee. Leslie Gilmore, Robert Dulfer, Ray Rasker, and Andy Derocher provided field assistance. Pat Mills typed the thesis and Engel Rahs prepared the graphics. Dr.John Elliott proposed the research problem and helped me to get started. Dr. W. Samuel provided the services of his laboratory for the parasitology analyses and Dr. T.M. Ballard provided the laboratory analyses of mineral levels. Members of the Guide Outfitters Association of British Columbia, particularly Ed and Dave Wiens and Blaine Southwick, provided information and assistance in conducting the study. Essentially everyone in the Toad River area, particularly Bruce and Donna Powell and the Price family, regularly helped me out. My thanks to all of you. Funding for this work was provided by the Canadian National Sportsmen's Fund, the Guide-Outfitters Association of British Columbia, the Foundation for North American Wild Sheep, and the Arctic and Alpine Research Committee (UBC).

STUDY AREA

The study was conducted in the vicinity of Toad River, British Columbia (59°N, 125°W) near Mile 422 of the Alaska Highway (Fig. 1). The study area included parts of the Muskwa Range and the Stone Range of the northern Rocky Mountains and extended into the Rocky Mountain foothills.

Geology of the area was discussed by Taylor and Stott (1973). The area is composed of bands of folded and faulted sedimentary rocks (shales, conglomerates, sandstones, and limestones) ranging in age from Precambrium in the southwest to Triassic in the northeast. The Precambrium formations in the southwestern part of the study area contain numerous igneous dikes, one of which was the site of a now abandoned copper mine.

Topography ranges from steep, precipitous, glacier-topped peaks in the southwest to more rolling country in the northeast. Elevations range from 750 m to 2500 m. Mountains have been extensively glaciated and exhibit cirques and U-shaped valleys. Talus slopes and alluvial fans create numerous open areas along forested slopes.

Soils in the area were described by Valentine et al. (1978). Generally the valley bottoms contain dystric and eutric brunisols, forested mountain slopes are composed of humo-ferric podzols, and the alpine peaks have regosol soils.

There is a permanent weather station maintained by the Federal Government within the study area at Muncho Lake. Long term, average weather data are summarized in Table 1.

The biogeoclimatic zones (Krajina 1976) of the area include the Boreal White and Black Spruce Zone which extends up to about 1400 m, the Spruce-Willow-Birch Zone between 1400 and 1600 m, and the Alpine Tundra Zone above 1600 m.

White spruce (*Picea glauca*) and black spruce (*P. mariana*) form the climax forest type at low elevations, but fire has induced the establishment of lodgepole pine (*Pinus contorta*), poplars (*Populus tremuloides* and *P. balsamifera*) and/or grassland in many areas depending on the fire frequency (Parminter 1981). Bearberry (*Arctostaphylos uva-ursi*) and mountain cranberry (*Vaccinium vitis-idaea*) are common ground cover at low elevation, and Labrador tea (*Ledum groenlandicum*), buffalo-berry (*Shepherdia canadensis*), high-bush cranberry

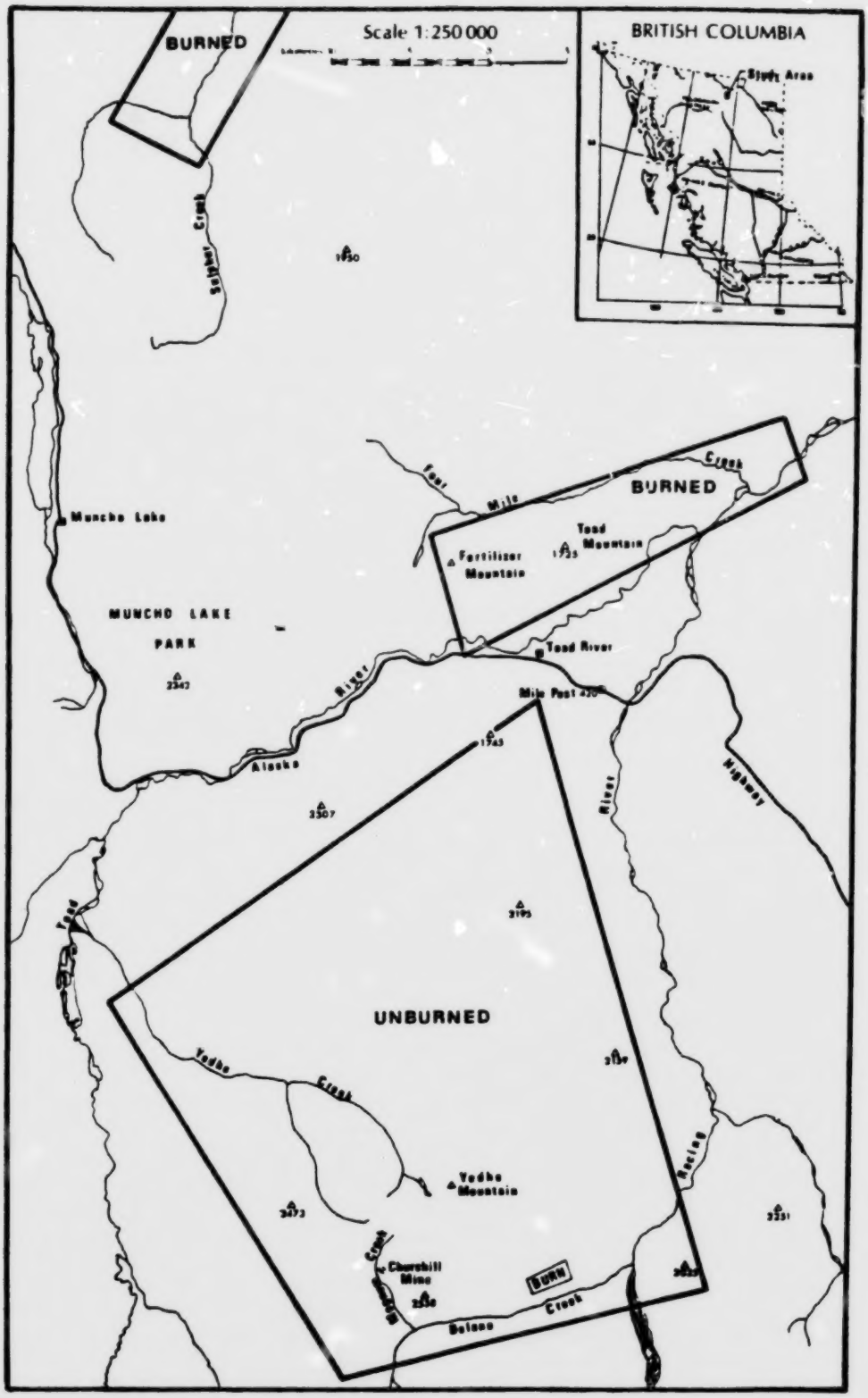

Figure 1. Location and map of the study area. Elevations in meters.

Table 1. Average climatic data for Muncho Lake, British Columbia (1955-1978).

Month	J	F	M	A	M	J	J	A	S	O	N	D	Total
Daily maximum temperature[a]	-13.0	-7.3	-2.0	6.7	13.4	18.2	20.2	18.7	13.6	6.9	-2.5	-10.1	-
Daily minimum temperature	-24.4	-19.8	-16.3	-6.1	0.6	5.7	7.7	6.1	2.1	-2.9	-12.2	-20.6	-
Average daily temperature	-18.7	-13.6	-9.2	0.3	7.1	12.0	14.0	12.5	7.9	2.1	-7.4	-15.4	-
Rainfall[b]	0.9	0.0	0.4	0.8	35.7	59.7	78.0	58.3	38.5	15.5	5.7	0.4	293.9
Snowfall	27.4	27.3	17.0	6.1	4.7	0.4	1.0	0.0	0.9	9.8	21.2	28.6	144.1
Total precipitation	35.2	33.3	19.9	6.8	43.0	60.2	79.4	58.3	39.0	23.8	27.3	32.8	459.0
Days with precipitation	12	9	9	4	7	11	13	13	13	10	9	10	120

[a] temperatures in °C.

[b] rain and snow in mm of water.

(Viburnum edule), willows (Salix spp.), alders (Alnus spp.), and rose (Rosa acicularis) are common shrubs.

The Spruce-Willow-Birch Zone is a transition zone from spruce forest to a shrubby zone dominated by scrub birch (Betula glandulosa) and willows. The Alpine Zone is dominated by mountain avens (Dryas integrifolia), sedges (Carex spp.), net-veined willow (Salix reticulata), and numerous lichens and forbs. This zone is discussed in detail in the results section.

A partial plant collection for the area was made by Gilmore (1981) and is located in the University of British Columbia herbarium. A more complete collection by A. Ceska in 1982 is located in the B.C. Provincial Museum Herbarium. Plant classification in the text is from Porsild and Cody (1980).

Sheep populations in parts of the Toad River, Racing River, and Sulphur Creek area (Fig. 1) have access to extensive areas of burned range. Sulphur Creek valley was intentionally burned by the B.C. Fish and Wildlife Branch in 1978. Analysis of fire scars on trees indicated that the Toad and Racing River valleys have experienced regular fires over the past 80 years at intervals of about 9 years (Parminter, pers. comm.). Most of these fires were intentionally started to create rangeland and several fires were started during the course of this project. Sheep in the Yedhe and Delano valley area are primarily found on unburned range except for a small (5 km^2) recent burn in the Delano valley. Otherwise the area shows no evidence of fire for at least the past 120 years (Parminter, pers. comm.).

Other large ungulates in the study area include moose (Alces alces), caribou (Rangifer tarandus), elk (Cervus elaphus), mule deer (Odocoileus hemionus), and mountain goats (Oreamos americanus). A bird and mammal list is located in Appendix A. Mammal classification is from Banfield (1974).

METHODS

RANGE USE PATTERNS AND GROUP COMPOSITION COUNTS

Sheep were regularly located by hiking and climbing throughout the area. These observations were supplemented with several helicopter and fixed-wing surveys throughout the season:

May, 1980	fixed wing
August, 1980	helicopter
March, 1981	fixed wing
April, 1981	fixed wing
July, 1981	helicopter
October, 1981	helicopter
February, 1982	helicopter
April, 1982	fixed wing
November, 1982	fixed wing

Conversations with local residents, outfitters, and Dr. John Elliott of B.C. Fish and Wildlife Branch were helpful in learning where to locate the sheep.

Counts and locations of sheep were recorded along with as complete a classification as was possible under specific conditions. For the unburned area, I used only lamb:yearling:ewe ratios which were collected in July at a major mineral lick (Churchill Mine) where a large sample size could be observed repeatedly (Fig. 1). For the burned range, the only composition counts in which I had confidence were winter counts which could be taken repeatedly from a group which remained on the same slope (Fertilizer Mountain) throughout winter and spring. The winter count was also the only one for which I could be confident that the counted sheep had used burned range in winter. For counts on alpine summer range, it was impossible to know where the sheep had wintered.

RANGE ANALYSIS

Forage biomass of ranges was measured by clipping all the plant material from 6-10 randomly selected plots. Most plots were 0.25 m^2 but occasionally 1 m^2 plots were used in alpine areas with very low biomass. The samples were sorted into live forbs, live graminoids, and standing dead material and then air-dried for several days until a constant weight was maintained. These samples were weighed to the nearest 0.1 g. Some samples (n = 53) were oven-dried at 100°C and then weighed. From this

information a correction factor equal to 92.5% ± 0.41 (SE) was calculated to convert air dry weight into oven dry weight.

Tiller length of grasses and sedges was measured by randomly selecting 10 or more individual tillers and measuring to the nearest mm the length from the ground to the tip of the longest leaf. Species composition of ranges was measured by a modified point transect method. A pointer was dropped at random intervals along a transect and the plant species hit by the pointer was recorded. The procedure was continued for 50-100 points/transect. The procedure was repeated until the average of the pooled data for all the transects stabilized and additional transects had no great effect on the average values.

Samples of graminoids, forbs, and browse were collected throughout the season for quality analysis. Only leaves were collected from browse plants but for graminoid and forb samples, all the plant parts were included. Samples were air dried for storage. In vitro digestibility, proximate analysis, and protein analysis was conducted by the Wildlife Habitat Laboratory, Washington State University, Pullman. In vitro digestibility was determined by the two-stage Tilley and Terry (1963) method utilizing rumen fluid from domestic sheep.

Mineral analysis of forage samples was done by the Department of Soil Science, University of British Columbia.

SOIL ANALYSIS

Samples of soil from various ranges as well as several mineral licks were collected for analysis. Litter was cleared away and a sample of the top 15 cm of soil was collected. Analysis was carried out by the Department of Soil Sciences, University of British Columbia. Exchangeable Ca, Mg, and K were determined by desorption in 1N NH_2OAc. Total carbon was determined using the Walkley-Black technique and phosphorous was determined using the Bray technique.

FECAL ANALYSIS

Fecal samples were air dried after collection. Nitrogen, ash, and DAPA analysis was done at the Wildlife Habitat Laboratory, Pullman. DAPA is a peptide found in the cell walls of rumen bacteria that is not absorbed by ruminants. The amount of DAPA in the feces is thus related to the rate of rumen microbial action and correlated with digestible energy intake (Nelson et al. 1982).

FOOD HABITS

Food habit analysis included fecal fragment analysis, rumen analysis, and direct observation. The rumen samples were collected from 5 animals that died from accidents. Rumen samples were stored in formalin and fecal samples were air dried. Analysis of rumen and fecal samples was done at the Wildlife Habitat Laboratory, Pullman. The technique for both rumen and fecal samples involves preparing a slide from a solution of the material, staining the slide, and identifying plant material at 300 random points on the slide using characteristics of epidermal tissue. For details see Nelson and Davitt (undated).

In addition, some information on food habits was collected by observing sheep feeding. It was usually very difficult to see what an animal was eating when it was grazing but it was easy to determine which plants were being browsed.

PARASITOLOGY

Fecal samples were collected from burned and unburned ranges in mid-winter and early spring. Samples were air dried for storage. Parasite counts were done by Dr. W. Samuels, University of Alberta, Edmonton, using the Baermann technique for recovery of first-stage larvae.

FORAGING BEHAVIOUR

Time budget information was collected by scanning the population every 5 or 10 minutes and recording the behaviour of each individual. Observations were made at distances ranging from 500 m to 5 km using 20-40X telescopes. Observations extended from dawn to dusk. Days with incomplete data caused by losing sight of the animals for long periods of time were excluded from

analysis. Loss of visibility was regularly caused by weather or animal movement. Most scans were done at a 5-minute interval except for several done in the winter of 1982 when I was doing daylong scans alone and it was too cold to maintain a 5-minute interval. For most scans, two observers worked alternating 2-hour shifts.

On each scan, behaviour of each individual was classed as:

i) foraging: head down and feeding or digging for food within approximately 3 seconds of spotting the animal.

ii) resting: lying down, often ruminating.

iii) standing: standing with head up for more than 3 seconds after being spotted.

iv) travelling: head up and moving for more than 3 seconds after being spotted.

These four behaviours accounted for the vast majority of the observations. Other activities (e.g., social interactions, comfort movements) comprised a very small amount of time in the day of a Stone's sheep. Behaviour of rams was recorded separately from behaviour of ewes and yearlings. Ewe and yearling data were aggregated because these classes occurred together in feeding groups and it was not always possible to distinguish accurately between the two classes given the observation conditions and time constraints imposed by maintaining a 5-minute scanning interval.

In winter, a large part of the foraging time was spent digging through the snow. Digging time in different snow depths was measured by observing individual sheep for 3-4 minute foraging periods and recording the amount of time spent digging. Snow depth was estimated by comparing the snow level to nearby sheep used for scale (Geist 1971).

Biting rate was determined by observing an individual ewe foraging for repeated 1-2 minute intervals and counting the number of bites taken. A bite was identified by a distinct jerking motion of the sheep's head which accompanied each bite. The counts were recorded on a tape recorder and transcribed later.

Foraging behaviour recorded during time budget observations included searching and chewing in addition to actual feeding time. The proportion of time actually spent feeding was determined from the biting rate tapes by

timing the time spent biting compared to the total foraging time.

Initially, biting rate was recorded once every 5 minutes for the same sheep throughout the entire day. However, analysis of these data showed no significant change throughout the day or during a foraging bout (see Results). Therefore, for subsequent counts, the observations were made over approximately a one hour period around mid-day.

CAPTURING AND MEASUREMENTS

The only place that I considered a feasible location to capture sheep was an abandoned copper mine site which was extensively used by sheep as a mineral lick in summer. In excess of 100 sheep used this area in June and July and were quite easy to approach. Sheep were captured in late June and early July of 1981 and 1982. In 1981, a cage trap was constructed of lumber and fishing net. The trap door was held up by a rope which could be released by hand to drop the door. The trap was baited with salt. Captured sheep were manually restrained and blindfolded. Measurements of hind foot length, chest girth, chest height, shoulder height, and horn length were taken for all animals. Lambs and yearlings were weighed by suspending them from a spring balance, but adult ewes struggled too much to be handled easily. Numbered collars were attached to adult ewes.

In 1982, sheep were captured in rope leg snares. Rope snares were laid out on the ground and sheep were baited into the area with salt. When one stepped into the noose the rope was pulled up by hand thereby catching the leg. The sheep were then wrestled to the ground. Measurements were taken as in 1981 except that adult ewes were tranquilized with 1 ml (4 mg/kg) of Rompun (xylazine hydrochloride) to allow weighing.

Horn growth data were obtained from B.C. Fish and Wildlife Branch compulsory reporting forms for hunter killed sheep in the area from 1976-1981.

RESULTS

RANGE USE PATTERNS

Winter Range

Most Stone's sheep in the study area used windswept mountain peaks and ridges as winter range (Fig. 2). Surveys of the Yedhe, Delano, and Racing River areas in February 1982, March 1981, and April 1982 found almost all the sheep (n = 140) to be using such ranges. These ranges were at elevations ranging from 1500 to 2200 m. The primary characteristic of these areas appeared to be their tendency to be blown free of snow. Such habitats appeared to be quite limited. In a survey area exceeding 1000 km^2, all the sheep located were using a total of less than 3 km^2. Most areas that were blown clear of snow and appeared to be suitable contained sheep or sheep tracks. No sheep were located on slopes with high snow accumulations. The one example of tracks in such areas was a single-file trail through a valley leading from one windswept peak to another. In March of 1981, 5 sheep were spotted in the Delano burn using areas that had melted clear of snow. However, in the winter of 1982, no sheep or tracks were seen in the Delano burn, presumably due to high snow accumulation (> 1 m).

The Toad Valley contains large areas of fire-induced, subalpine grassland. In March of 1981, these subalpine slopes were snow-free and were used by about 40 sheep. However, in the winter of 1982 (January-April), most of these slopes were snow-covered and unused by the sheep. Rather, the sheep were regularly spotted (102 sightings) using the windswept peak of Toad Mountain. Similarly, in the Sulphur Creek valley, the large areas of burned range were snow-covered and unused and the sheep were located (n = 11) on the snow-free peaks of adjacent mountains. The exception was one slope on Fertilizer Mountain which was a subalpine, burned slope which remained partially snow-free throughout the winter due to its particular combination of steepness, south-facing aspect, and parallel orientation and exposure to the prevailing winds (Fig. 3). This small snow-free area of about 5 ha supported about 33 sheep throughout the winter. Thus, the general pattern of winter range use was that Stone's sheep sought out low-snow or snow-free areas and avoided deep snow areas. In most places this meant using high windswept mountain peaks. Low elevation slopes, including burned slopes, were generally unavailable as winter range due to high snow accumulation except in low-snowfall years or in

Figure 2. Windswept, alpine winter range in the Yedhe area (February 1982).

Figure 3. Burned subalpine winter range (Fertilizer Mountain) in a high snowfall year (February 1982).

atypical locations. When flying over Stone's sheep country in winter, the overall impression was of immense areas of empty, barren mountains covered in deep snow with the sheep restricted to small, scattered patches of desolate, snow-free mountain tops.

The vegetation atop the wind-swept, alpine peaks used as winter range was very sparse and largely composed of lichens (Alectoria spp., Cetraria spp., Cladina spp.), sedges (Carex spp.) and some grasses (primarily Festuca altaica and Poa spp.). The vegetation on the subalpine, burned slopes was primarily ryegrass (Elymus innovatus) with lesser amounts of other grasses (Agropyron spp., Poa spp.) and forbs (Artemisia frigida, Oxytropis spp., Vicia spp.).

The effect of snow on sheep distribution was most easily observed on Fertilizer Mountain which was visible from my camp. In 1982, the slope was used by approximately 26 sheep. For most of the time after I arrived in late February, the entire slope was snow-free and sheep ranged over the entire area (115 sightings). When the slope was snow-covered for 2 days following a snowstorm in early April, all the sheep restricted their activity to small areas of the total range, primarily along rocky outcrops and cliff edges on which snow shedding and melting was accelerated. Use of the entire range resumed immediately after snow melt. In the winter of 1982, most of the slope was covered in deep snow except for a small area that remained blown clear of snow. One could see bare exposed ground on this area even immediately following major snowstorms. Locations of sheep were observed twice each day throughout February and are shown on Fig. 4. Following snowstorms, the sheep would retreat to the central part of this area which would be essentially snow-free. They would initially feed in this area and then gradually radiate outwards by digging through the snow to feed. This activity left a packed area behind as the feeding sheep slowly advanced through the snow. From a distance it appeared as if the sheep were eating the snow off the mountain in a slowly expanding region. This activity continued until they reached areas in which the snow was quite deep so they ceased digging and returned to feed again in the packed area. Thus, the central part of this area was grazed over repeatedly throughout the winter.

The snow depth ($\bar{X}$ ± S.E.) at the edge where the sheep ceased digging for food was 32.4 ± 1.9 cm (range 23-40 cm). Snow depth beyond this boundary which was unused by sheep ranged from 23 to > 100 cm. The average snow depth within the area that was used by the sheep was 16.5 ± 2.1

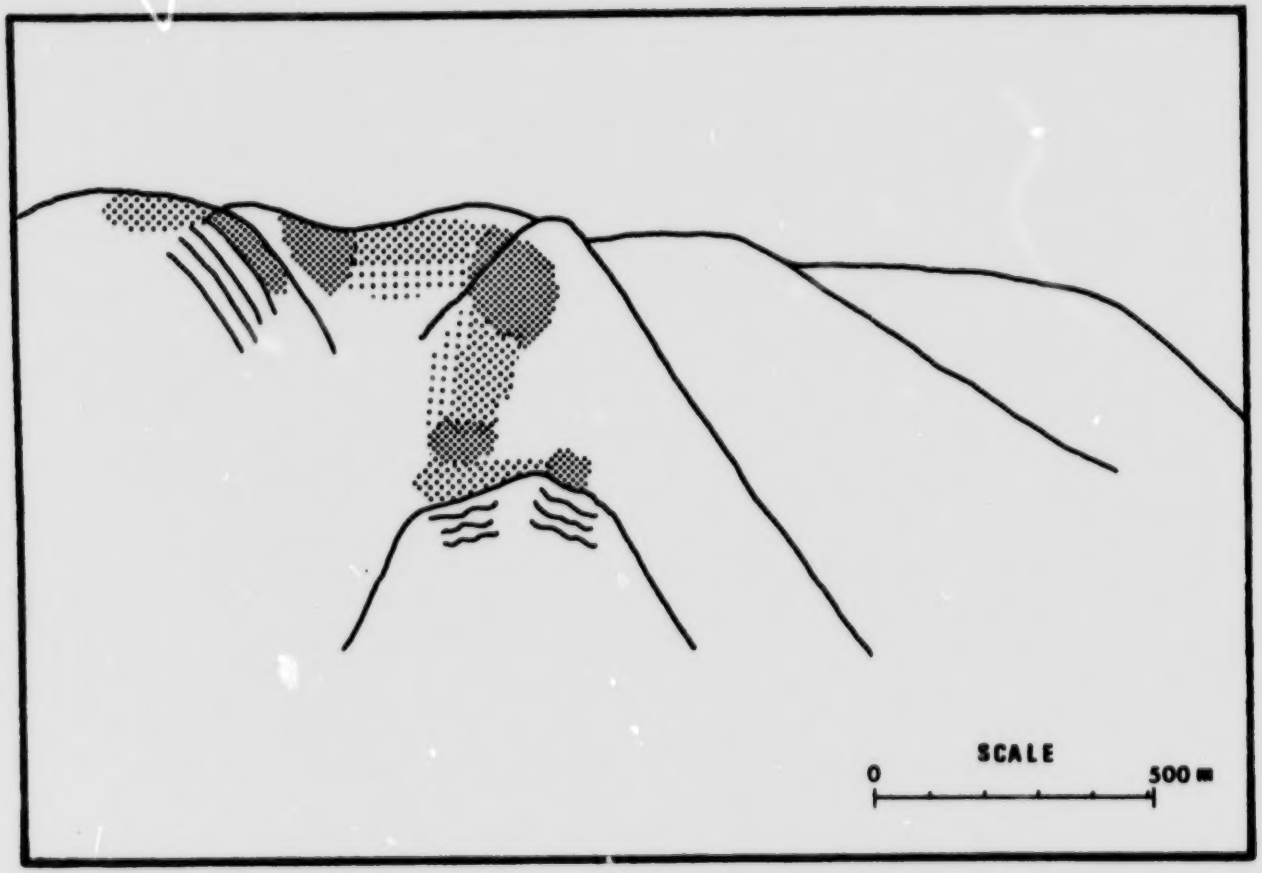

Figure 4. Use of winter range (January-March) on Fertilizer Mountain in a year of high snowfall (1982). Density of dots corresponds to intensity of use.

cm (range 0-26 cm). Thus it appeared that Stone's sheep were restricted to areas with less than 25-30 cm of snow in winter.

Spring Range

The sheep used low elevation (1200 - 1500 m) areas for spring range. In the Delano and Yedhe area, sheep primarily used natural subalpine clearings including streamsides, rockslides, talus slopes, and avalanche chutes (Fig. 5). In addition, the subalpine burn in Delano valley was also used by sheep in spring. The arrival of the sheep on these low elevation ranges from the alpine winter range occurred in late April. Similarly, sheep on Toad Mountain which wintered in the alpine moved down to the subalpine burned range (Fig. 6) at about the same time. The sheep on Fertilizer Mountain which wintered on subalpine burned slopes remained on the same slope throughout the spring although they ranged more widely once the snow no longer restricted their movement. They also occasionally moved to areas of the slope several hundred meters lower than those used in winter.

The species composition of the spring ranges is summarized in Table 2. Forage quantity and quality are discussed in subsequent chapters.

Sheep also selected spring range at a more fine-grained level. The sheep on the burned, subalpine range avoided areas with high amounts of winter carryover in spring and fed in areas that were largely free of carryover. Some of these areas lacked vegetation because it was removed by heavy grazing the previous winter whereas other areas lacked vegetation because they were naturally unproductive (e.g., cliff edges, outcrops). These areas could be visually identified from a distance by the dark colour compared to the golden brown of areas covered in senescent grass. Such areas had almost no carryover compared to 145 ± 17.2 (S.E.) g/m^2 on the unused areas. A scan survey of sheep feeding on Fertilizer Mountain in spring found 27 sheep feeding in areas with low amounts of carryover and 0 feeding in areas with abundant carryover.

Altitudinal Migration To Summer Range

Movement from spring range to summer range was a gradual process. In the Delano and Yedhe area the sheep moved from subalpine clearings in May to similar clearings in Spruce-Willow-Birch zone valleys in early June and to high alpine peaks by July (Fig. 7). Similarly, in the Toad River area, sheep moved from low elevation burned

Figure 5. Typical unburned spring range in Yedhe valley (May 1982).

Figure 6. Burned subalpine spring range on Toad Mountain (May 1982).

Table 2. Species composition (% cover) of Stone's sheep subalpine, spring ranges (May-June) in northeastern British Columbia (1980-82).

Plant Species	Burned Slopes		Natural Clearings	
	Delano	Fertilizer Mt.	Delano 1	Delano 2
GRAMINOIDS				
Elymus innovatus	40	57	10	9
SHRUBS				
Arctostaphylos rubra	-	-	-	5
A. uva-ursi	10	-	75	24
Betula glandulosa	-	-	-	9
Juniperus spp.	-	-	10	-
Populus spp.	11	-	-	-
Potentilla fruticosa	-	-	-	5
Rosa acicularis	10	t[a]	-	-
Shepherdia canadensis	t	-	-	t
FORBS				
Achillea spp.	t	t	-	-
Arnica spp.	-	-	-	t
Aster spp.	-	7	-	-
Dryas integrifolia	-	-	-	44
Epilobium angustifolium	5	-	-	-
Fragaria spp.	-	t	t	-
Galium spp.	t	t	-	-
Oxytropis spp.	-	9	t	-
Potentilla spp.	-	4	t	-
Saxifraga spp.	-	-	t	t
Silene spp.	-	-	-	t
Solidago spp.	-	t	-	-
Thalictrum spp.	-	5	-	-
Vicia spp.	-	t	-	-
OTHER				
Bare soil	18	-	-	-

[a] t= <2%

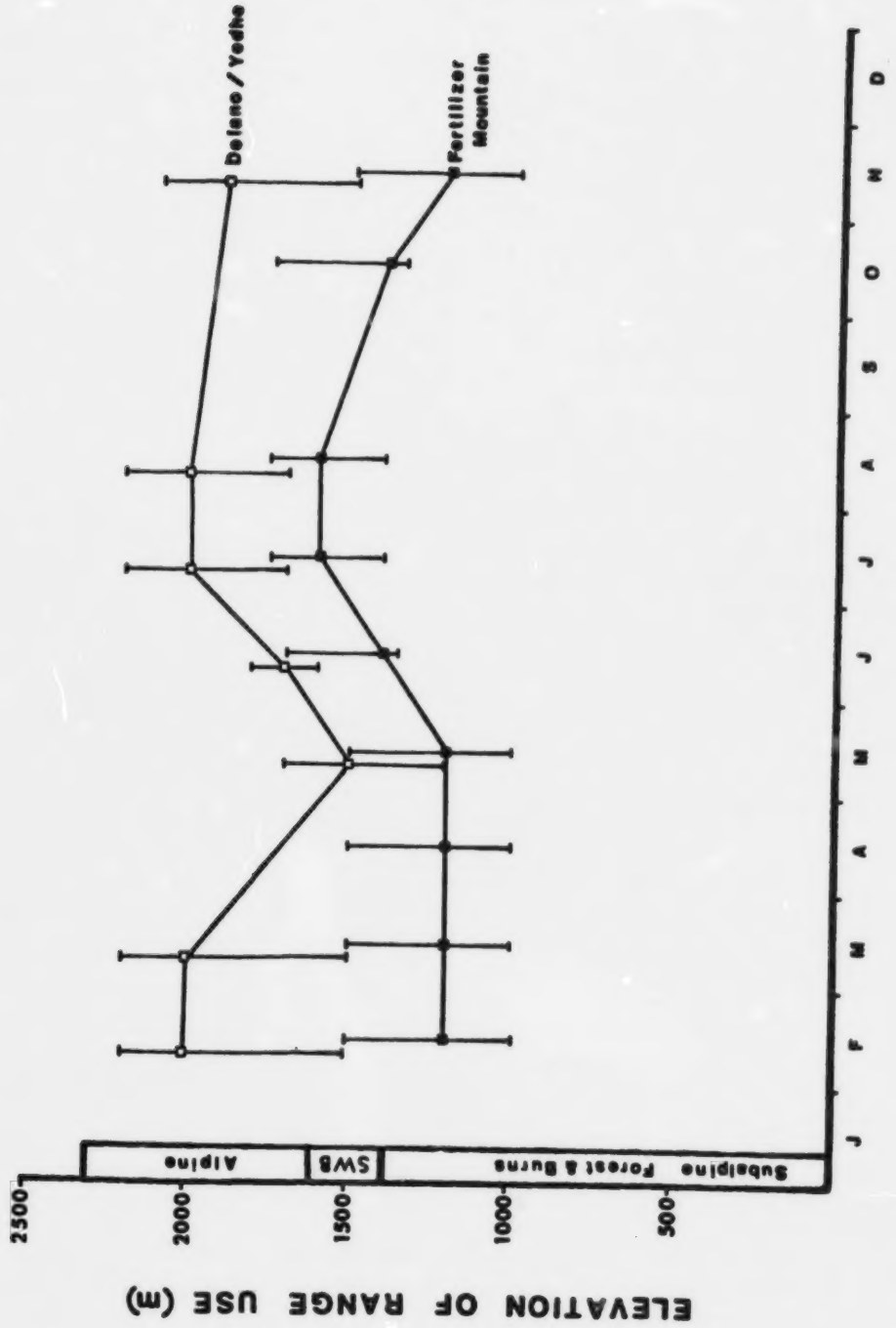

Figure 7. Elevation of range use (mode ± range) by Stone's sheep in northeastern British Columbia (1980-1982) throughout the year.

slopes in May to the Spruce-Willow-Birch zone in June and the high alpine in July (Fig. 7).

The migration corresponded to the onset of green-up at progressively higher elevations. The location of sheep during this period corresponded to areas where new grass had reached a height of approximately 10 cm. By the time the grass had grown longer the sheep had moved to higher slopes where production began later (Fig. 8). This movement continued until July at which time the sheep were found on high alpine peaks and ridges and there were no higher ranges available. Exceptions to this general pattern seemed to be related to movements to mineral licks which resulted in the animals being in areas for reasons other than foraging. This phenomenon is discussed later (Mineral Nutrition).

The species composition of the summer ranges is described in Table 3.

Fall Range

Range use was extremely variable during the fall with sheep being located from high alpine peaks to low, subalpine burned slopes in October and November. In November 1982, 54 sheep were sighted on high alpine peaks in the Yedhe/Delano area but during the same survey 20 sheep were using the Delano burn and an additional 44 sheep were using burned slopes along the Racing River. On Toad Mountain, 14 sheep were using the top ridge while 32 were using burned, subalpine slopes. Overall it appeared that sheep with access to burned, subalpine slopes made extensive use of them in fall whereas sheep without access to burns used the alpine.

Use of natural subalpine clearings in fall was not observed. Most of the sheep using subalpine burns in fall were in areas adjacent to important alpine wintering areas which were used when deep snow accumulated on the subalpine slopes.

Spatial Separation Of Sexes

Spatial separation of sexes was not apparent in the present study. Although rams tended to be in groups segregated from ewes and yearlings, both types of groups foraged on the same range. For example, the winter/spring range on Fertilizer Mountain supported 16 ewes, 8 lambs, and 9 rams in 1982. Although the group of 9 rams tended to stay together, they regularly foraged in the same area as the ewes and often the groups became completely intermixed. Similarly, most patches of alpine winter range

Table 3. Species composition (% cover) of several Stone's sheep summer ranges (June-July) in northeastern British Columbia (1980-1982).

Plant Species	Spruce-Willow-Birch	Alpine	
	Toad Mt.	Magnum Cr.	Fertilizer Mt.
GRAMINOIDS			
Carex spp.	-	9	15
Elymus innovatus	10	-	-
Festuca altaica	-	5	t
Poa spp.	t[a]	t	t
SHRUBS			
Arctostaphylos uva-ursi	6	-	-
Betula spp.	12	-	-
Ledum groenlandicum	4	-	-
Rhododendron lapponicum	17	-	-
Salix spp.	-	-	7
S. reticulata	-	11	-
Vaccinium spp.	7	-	3
FORBS			
Anemone spp.	-	5	-
Astragalus spp.	-	t	-
Cassiope spp.	-	t	-
Delphinium spp.	-	-	t
Dryas integrifolia	24	40	17
Lupinus arcticus	7	8	8
Pedicularis spp.	-	-	t
Polygonum spp.	-	4	t
Potentilla spp.	t	t	t
Pyrola spp.	t	-	-
Silene spp.	-	-	t
OTHER			
Lichens	-	-	28
Mosses	-	-	8
Equisetum spp.	-	-	t

[a] t= <2%

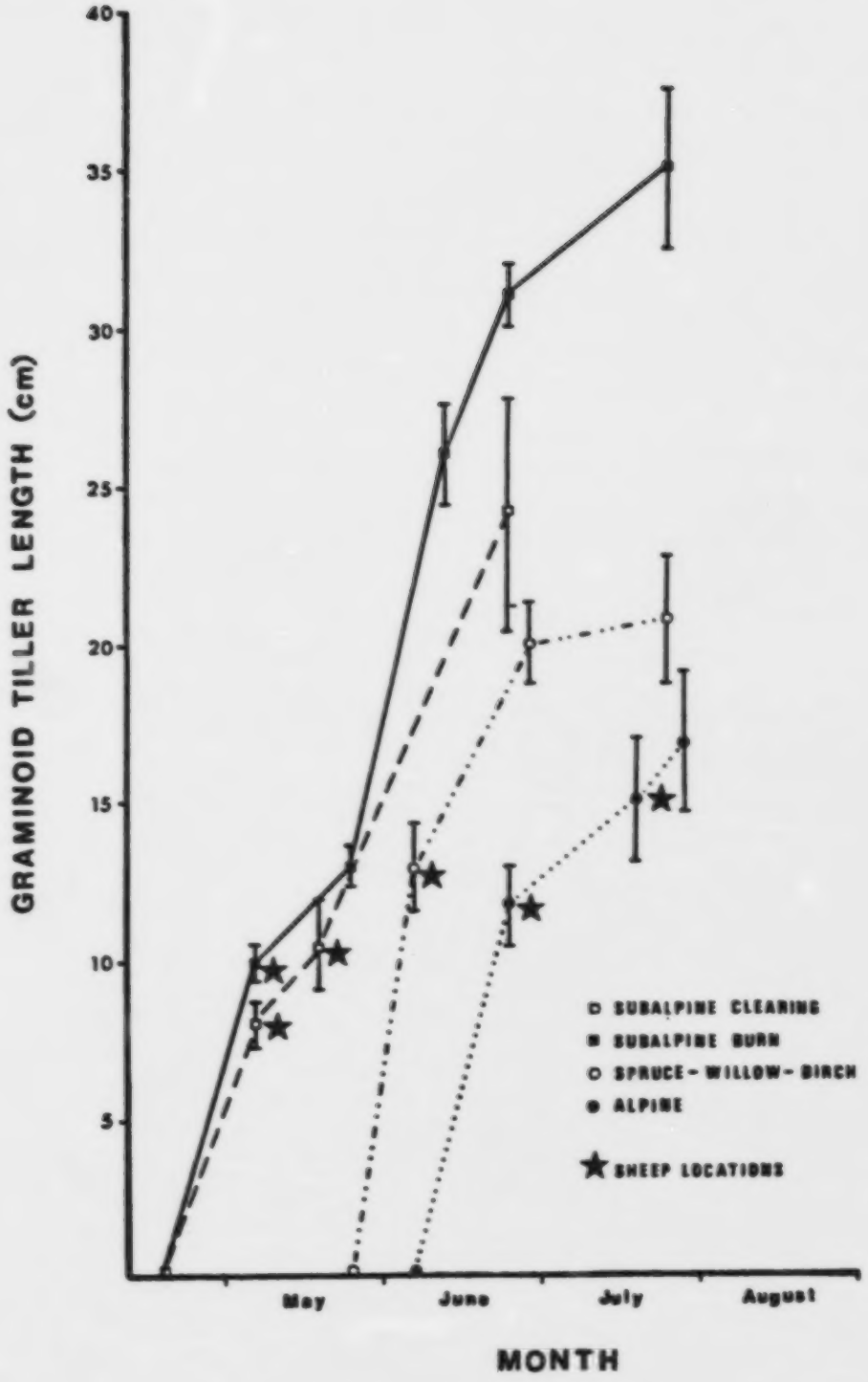

Figure 8. Relationship between tiller length of new grass ($\bar{X}$ ± 95% C.I.) and range use by Stone's sheep in spring and summer. Star indicates area where most sheep are located at that time of the year.

contained both rams and ewes living together on the same small areas. One extreme example was a large ram and a ewe alone together on an isolated peak in winter. Ram and ewe groups also used the same ranges in spring and summer and often inter-mixed. Overall, there was no reason to believe that spatial separation of sexes was a common phenomenon in these Stone's sheep.

FORAGE PRODUCTION AND BIOMASS ON STONE'S SHEEP RANGES

Pattern Of Production

The onset of major green-up of graminoids on subalpine, burned slopes in the area ranged from late April in 1980 to about May 5 in 1982. However, there was a limited amount of new production long before this time. In particular, scattered Oxytropis spp. and Artemisia spp. plants had begun growing by mid-March in 1981. Green-up on natural subalpine clearings occurred at the same time as on subalpine burns (Figs. 8 and 9). Therefore, sheep using these natural clearings could obtain new production as early as sheep on burned ranges. However, the quantity of new vegetation available in May on these natural clearings was much less than that available on burned slopes (Fig. 9).

The grass plants on the natural clearings were as tall as those on burned slopes (Fig. 8) but the density of plants was much less. Tiller density was calculated by dividing the standing crop of grass by the weight/tiller which was estimated from the relationship between tiller length and tiller weight (Fig. 10). The tiller densities in May calculated in this way were: 30 tillers/m^2 on natural subalpine clearings compared to 180 tillers/m^2 on burned subalpine slopes.

Early forb production on the slopes used as spring range included Oxytropis spp., Fragaria spp., Potentilla spp., Achillea spp., and Epilobium spp. By late May, Thalictrum spp., Vicia spp., Astragalus spp., Solidago spp., and Erigeron spp. were also growing.

The forb species were similar on both natural clearings and burned subalpine slopes (Table 2) but as with grass, the biomass of forbs was much higher on burned slopes (Fig. 11). Dryas integrifolia was not included in the measurement of forbs because although it often formed a complete ground cover, particularly in the alpine areas, it was only a minor component in the diet of the sheep. D. integrifolia was also extremely difficult to collect and sort. The amount of D. integrifolia on plots that

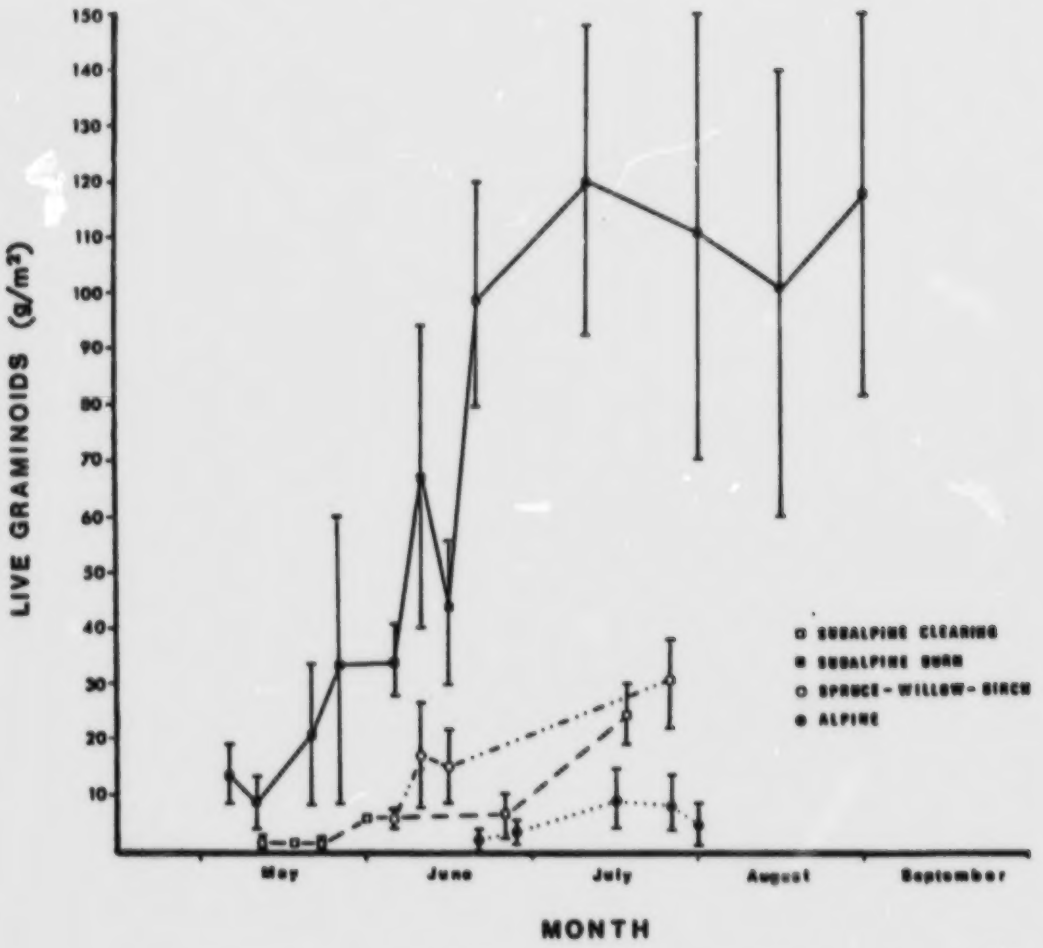

Figure 9. Seasonal pattern of graminoid production ($\bar{X}$ ± standard deviation) on Stone's sheep ranges in northeastern British Columbia (1980-1982).

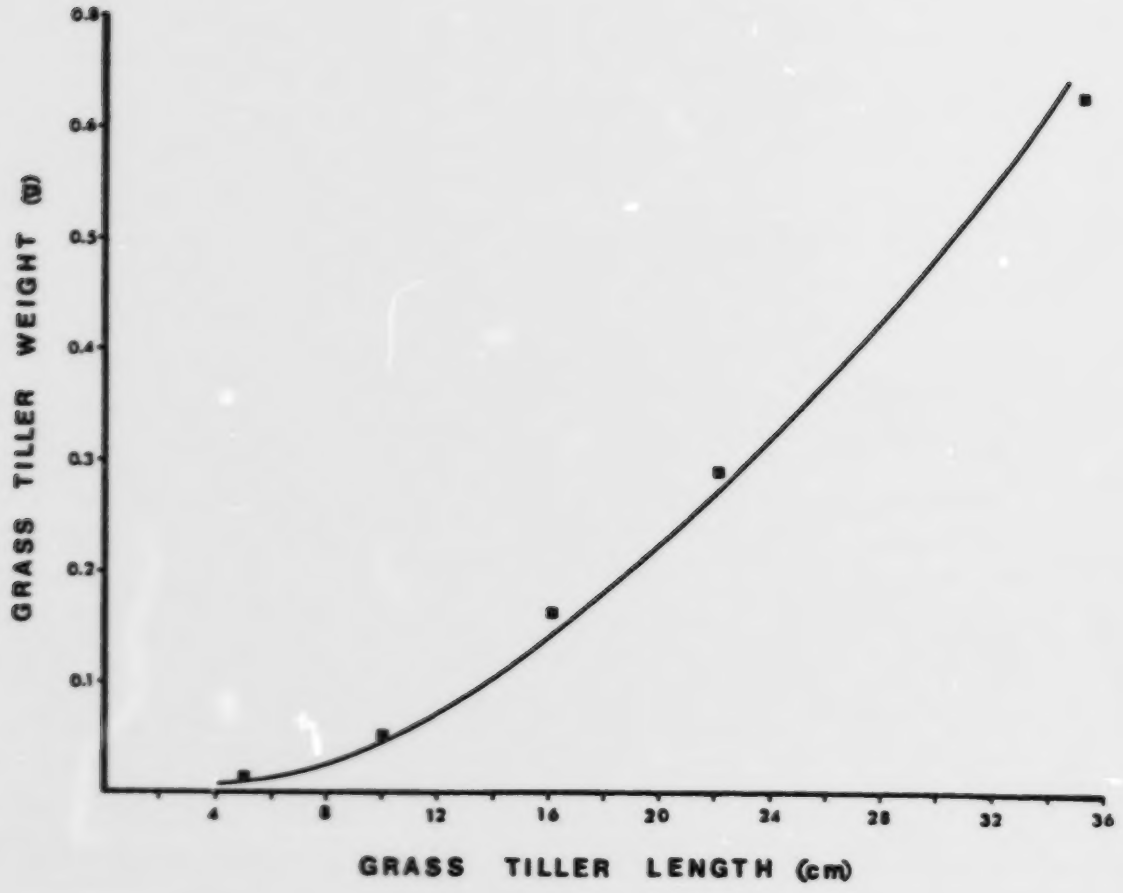

Figure 10. Relationship between mean tiller length and mean tiller weight of grasses on Stone's sheep subalpine spring ranges.

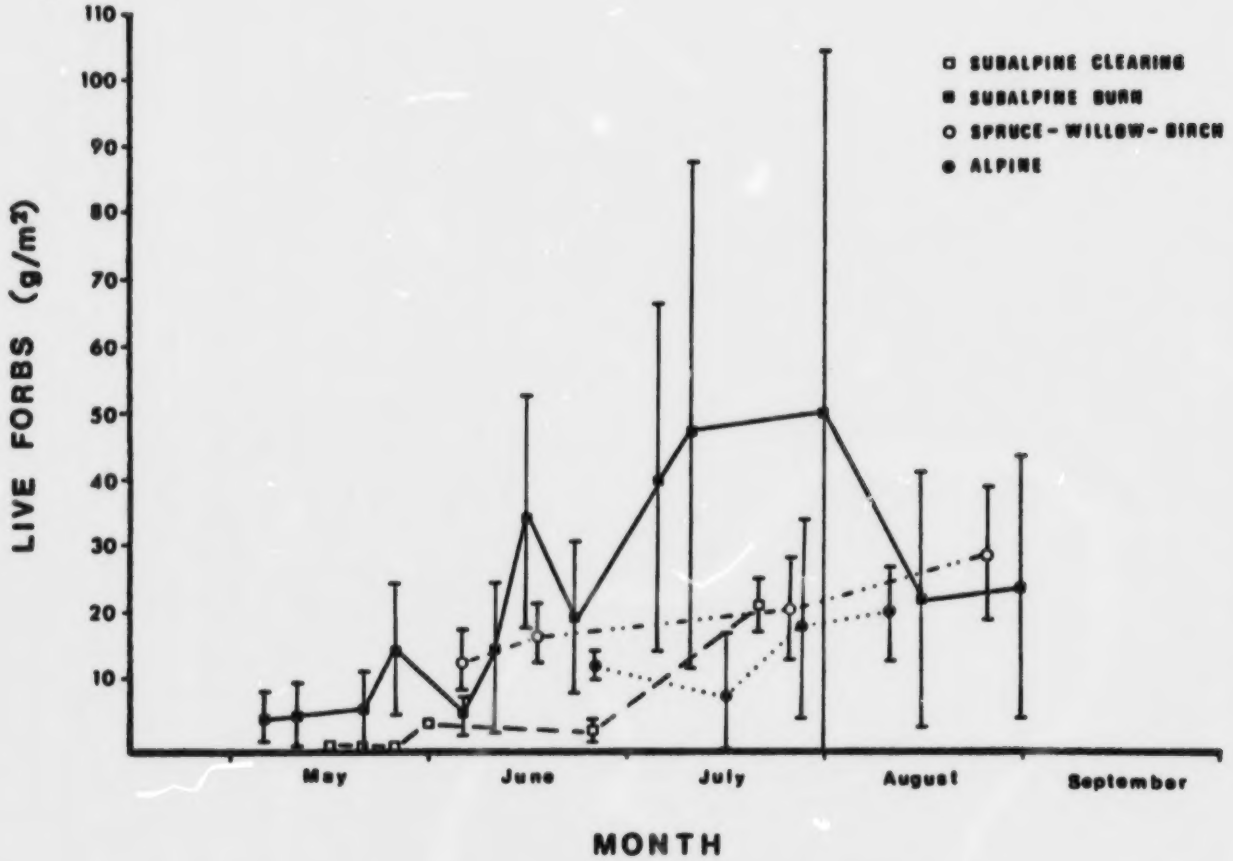

Figure 11. Seasonal pattern of forb production ($\bar{X}$ ± standard deviation) on Stone's sheep ranges in northeastern British Columbia (1980-1982).

were clipped was up to 30-40 g/m² for areas where it formed complete ground cover.

Leaf emergence on poplars (Populus tremuloides) and cottonwoods (P. balsamifera) began during the latter half of May on subalpine slopes. Browse biomass was not measured since it was essentially unlimited for any sheep which chose to feed on browse.

When the sheep moved upwards from the subalpine burns to the Spruce-Willow-Birch Zone in early June they were moving to an area of lower forage quantity and shorter tiller length (Figs. 8 and 9). Sheep moving up from the natural subalpine clearings were also moving to an area of shorter grass but forage quantity was similar. Leaf emergence on willows (Salix spp.) and birches (Betula glandulosa) in this area occurred in mid-June. When the sheep moved into the high alpine in July, they were once again moving to an area of short grasses and sedges and lower forage biomass.

Peak standing crop occurred in early July in the subalpine and late July in the alpine. The subalpine burns had by far the greatest quantity of forage but at this time the sheep were feeding on the sparse vegetation in the alpine.

Available green forage declined on all ranges after this time as vegetation gradually matured. By October, all vegetation had ceased growing and sheep had to feed on dormant vegetation for the duration of the winter.

Winter Range

Dormant vegetation was abundant on subalpine burned slopes in February-March (162.0 ± 17.5 g/m²) ($\bar{X}$ ± SE, n = 23). However, because these areas were usually snow-covered, this food usually was not available to the sheep. During the winter of low snow accumulation (1981) the sheep on Fertilizer Mountain were able to feed in areas of high forage quantity. However, in 1982, restriction of the sheep to a small area by snow resulted in them consuming virtually all of the forage from that slope. Immediately adjacent areas which had been snow-covered during the winter still had 97.6 ± 14.5 g/m² (n = 5) of standing dead vegetation remaining in spring. This heavy grazing of snow-free areas is obvious in Fig. 12.

Sheep wintering on windswept alpine ridges began with a much lower availablity of plant forage (Figs. 9 and 11), plus an undetermined quantity of lichens. Heavy grazing on these restricted ridges in the Delano and Yedhe area

Figure 12. Boundry between heavily grazed area and snow-covered, ungrazed area on subalpine winter range (Fertilizer Mountain 1982).

had removed essentially all the vegetation by late February of 1982. There was so little vegetation left that it was difficult to collect a few grams of plant material for laboratory analysis.

When these sheep moved down to natural subalpine clearings in the spring they encountered 24.8 ± 3.9 g/m² (n = 5) of standing dead vegetation in addition to whatever new growth was present.

FORAGE QUALITY

Winter Forage

Winter forage was high in fibre (ADF) and lignin and low in protein and digestibility (Figs. 13 - 15; Table 4). Statistical comparisons were based on comparison of the confidence intervals in the graphs. There was no difference ($P > 0.1$) between the quality of alpine and subalpine winter forage; it was equally poor in both areas. There was an indication that the winter forage remaining on the heavily grazed areas was poorer in quality than the forage on ungrazed areas that had been covered in snow and unavailable to the sheep. Remaining forage in the heavily grazed areas was lower in protein, digestibility, and cell contents and higher in fibre (ADF) and lignin than forage from ungrazed areas. Although these differences were not statistically significant, they do suggest that heavy grazing resulted in a decreased quality of the forage remaining for the animals. Most of this remaining material in areas of heavy grazing was hard stems compared to dry leafy material available in the ungrazed areas.

Spring-Summer Forage

The appearance of new production in spring provided a dramatic increase in the quality of forage available to Stone's sheep. There was no difference in forage quality between the burned, subalpine ranges and natural, subalpine clearings used by sheep in May (Figs. 13-15).

As the growing season progressed, there was an overall tendency for protein levels to decrease and fibre and lignin levels to increase in both graminoids and forbs (Figs. 13-18). The decrease in nutritional quality of grasses throughout the growing season was also shown by the negative relationship between grass tiller length and protein content (Fig. 19). Compared to the phenologically older subalpine vegetation, vegetation at higher elevations started to grow later in the season and

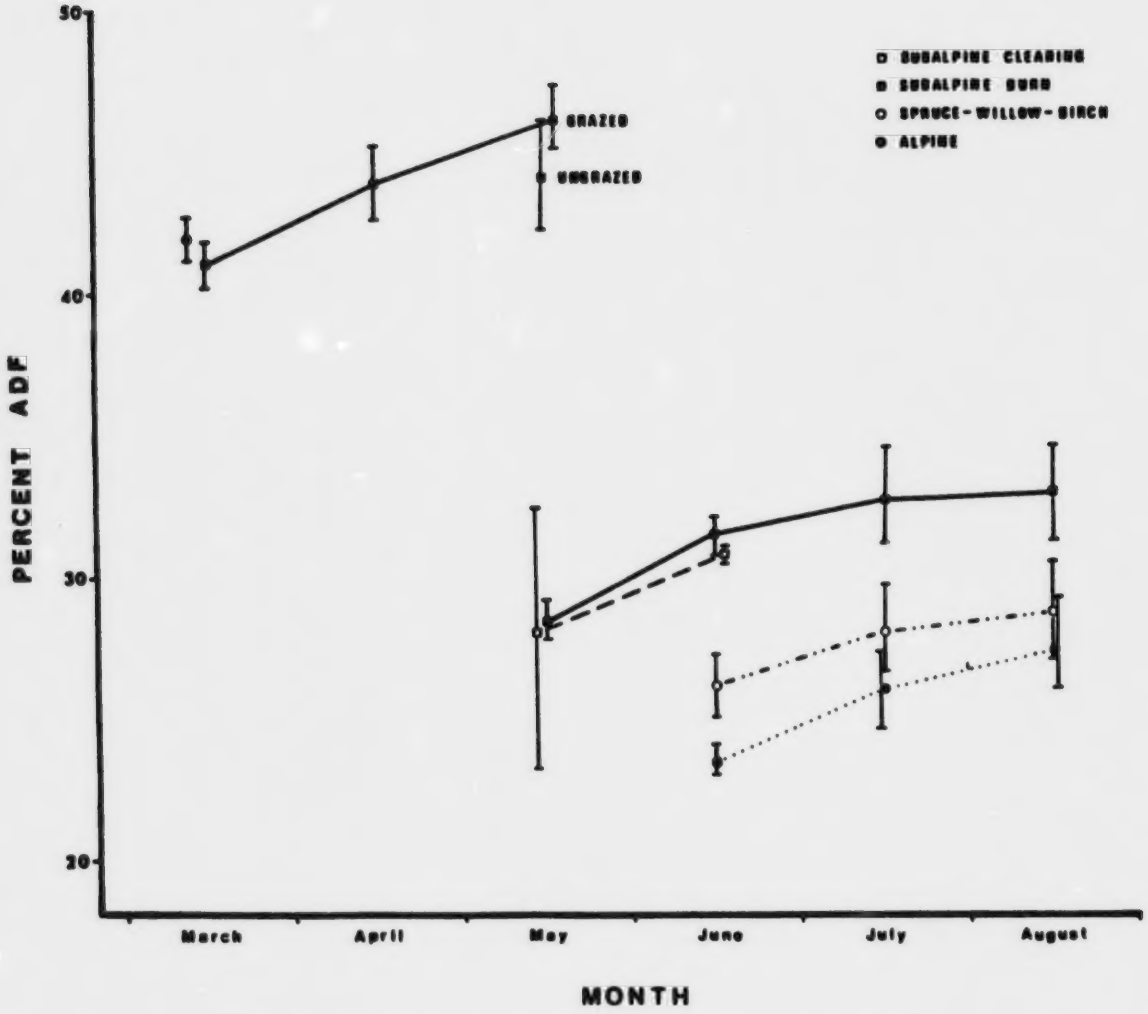

Figure 13. Seasonal pattern of ADF concentrations in graminoids ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

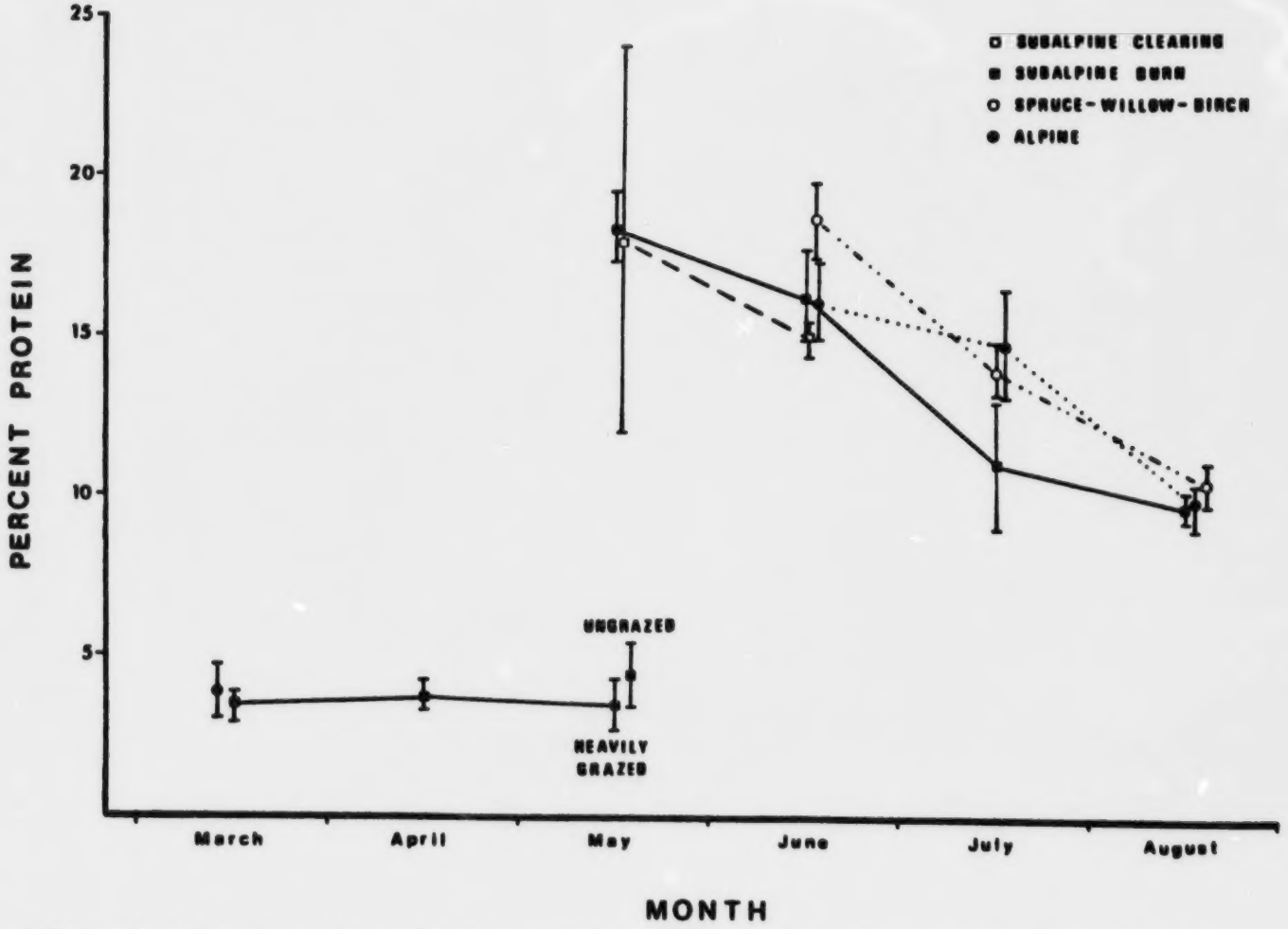

Figure 14. Seasonal pattern of crude protein concentrations in graminoids ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

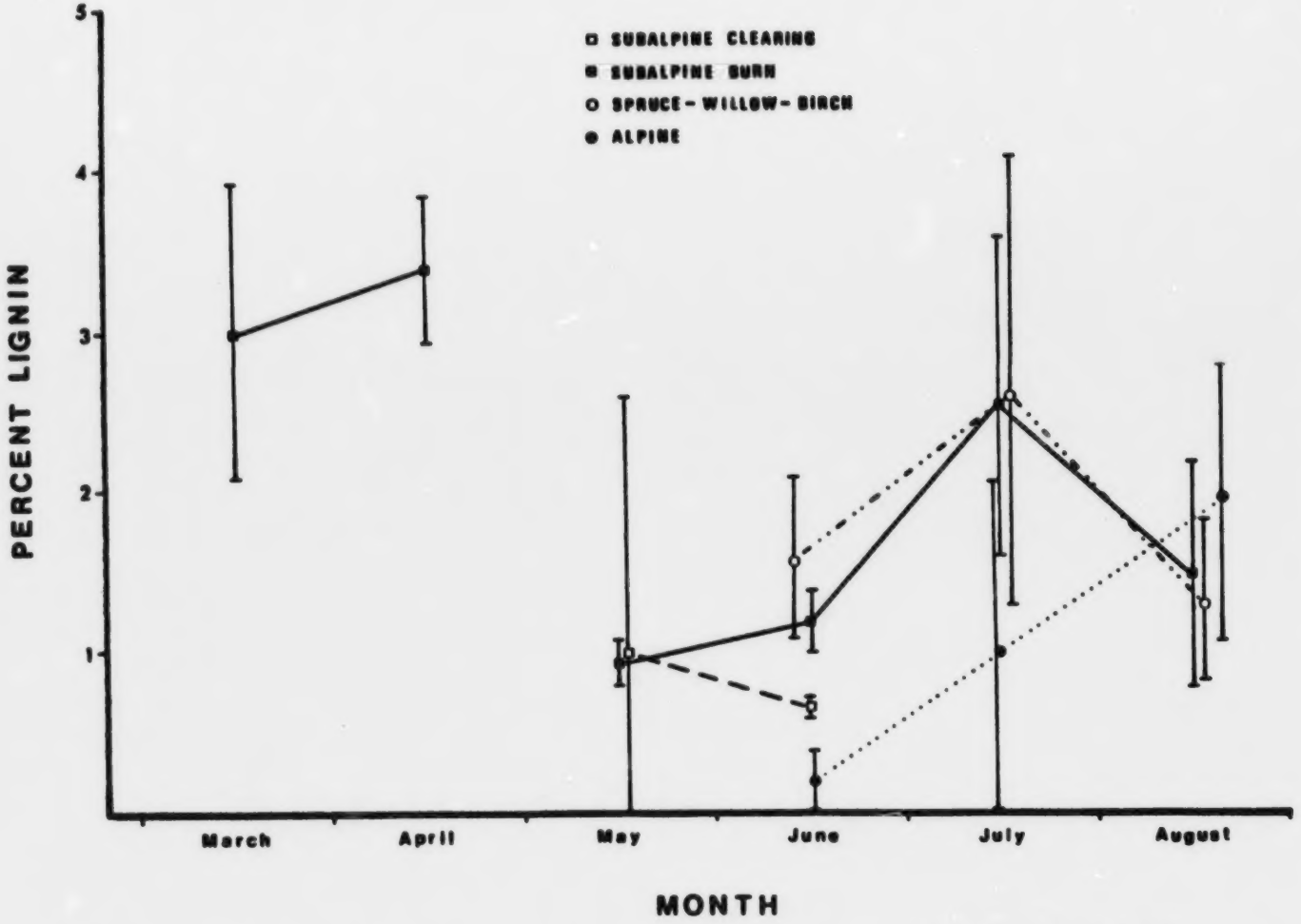

Figure 15. Seasonal pattern of lignin concentrations in graminoids ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

Table 4. In vitro dry matter digestibility (%) of graminoids and forbs from Stone's sheep ranges in northeastern British Columbia (1980-1982).

Location	Graminoids ($\bar{X} \pm SE$)	n	Forbs ($\bar{X} \pm SE$)	n
Winter Range:				
subalpine burned -heavily grazed	36.5± 2.6	4		
-ungrazed	39.8± 3.7	5		
alpine	32.1	1		
Spring Range:				
subalpine burn -May 25	65.1± 0.4	3		
-June 3	51.9± 3.7	3	53.2	1
June 25	43.3± 5.2	3		
subalpine clearings May 15	56.2	1		
June 25	48.0	2		
spruce-willow-birch June 7	50.5	1	48.4	1
June 25	57.0± 0.2	4		
Summer Range:				
alpine June 25 *Carex*	53.8± 1.8	4	59.7± 2.6	3
June 25 *Festuca*	55.3	2		
August 1	57.0± 2.5	7	66.5± 2.1	8

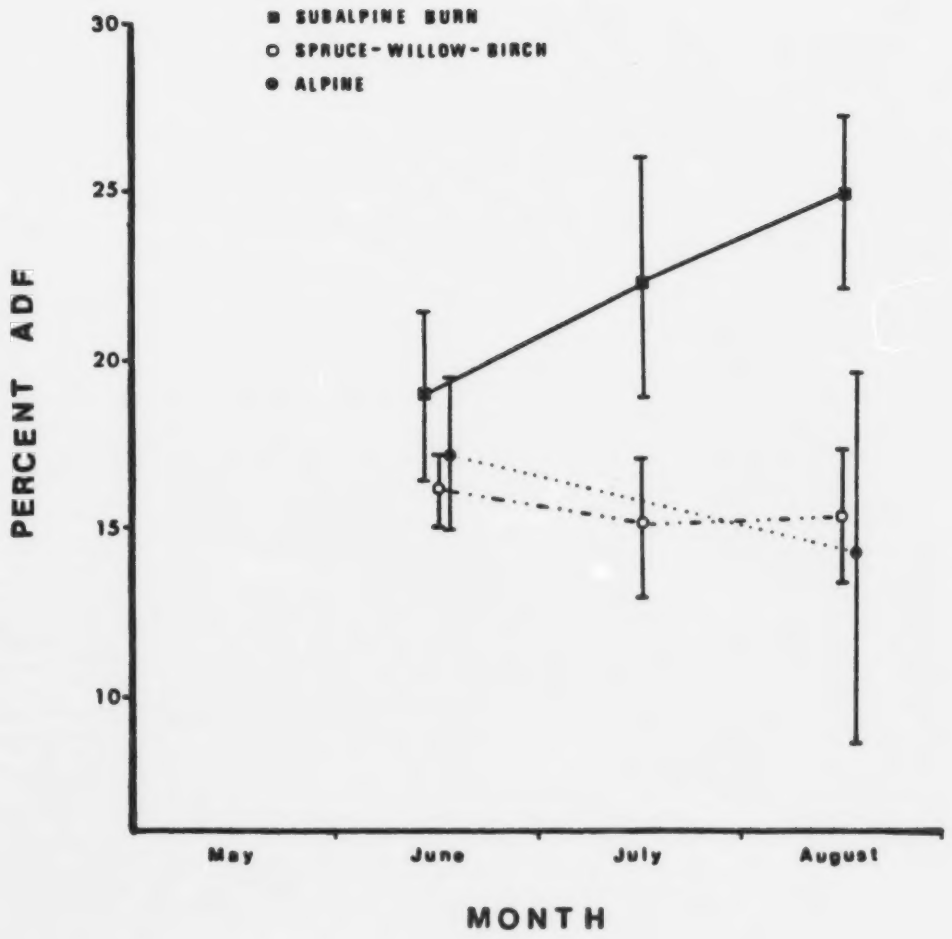

Figure 16. Seasonal pattern of ADF concentrations in forbs ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

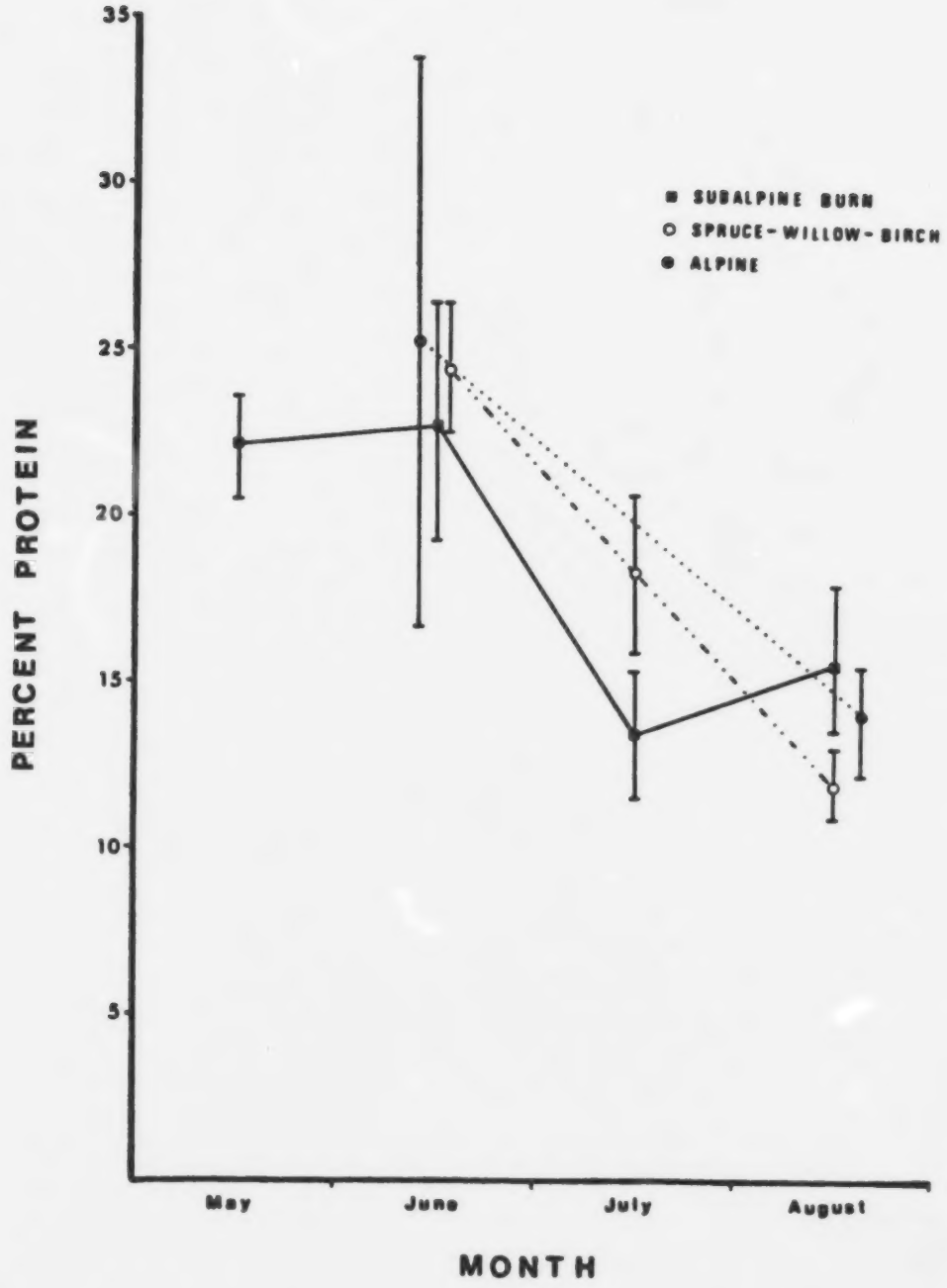

Figure 17. Seasonal patterns of crude protein concentrations in forbs ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

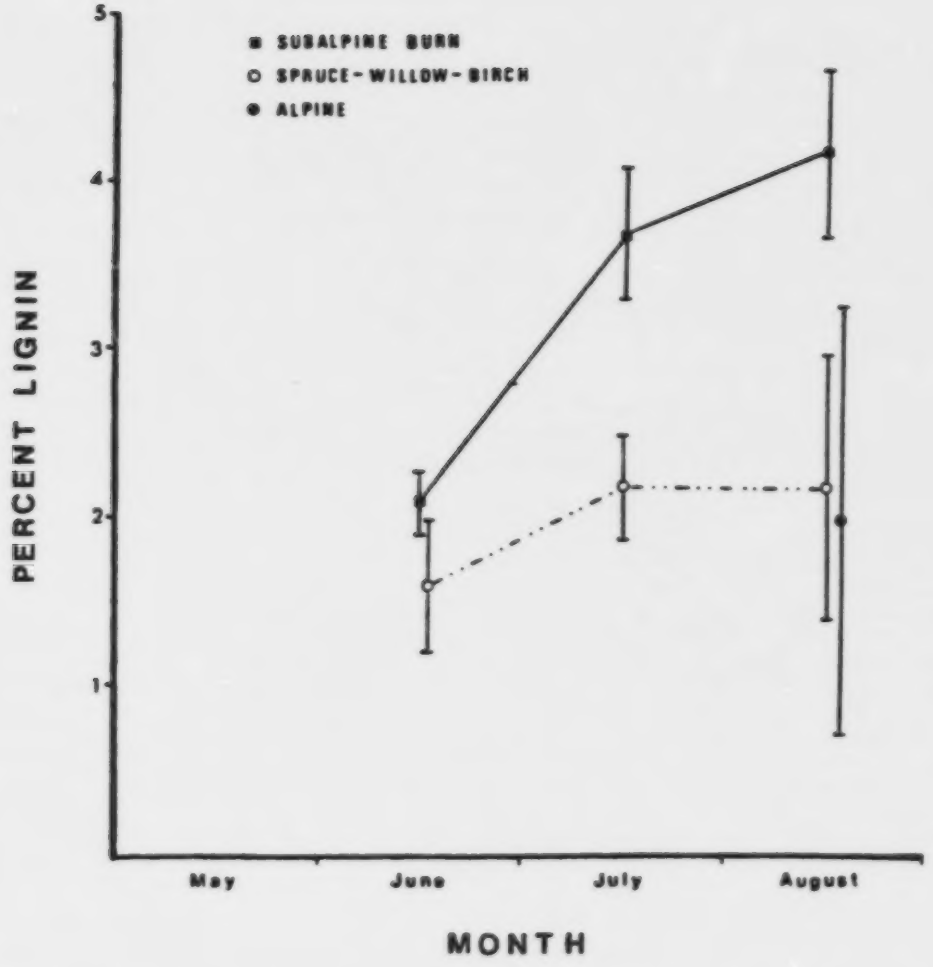

Figure 18. Seasonal pattern of lignin concentrations in forbs ($\bar{X}$ ± 90% C.I.) on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

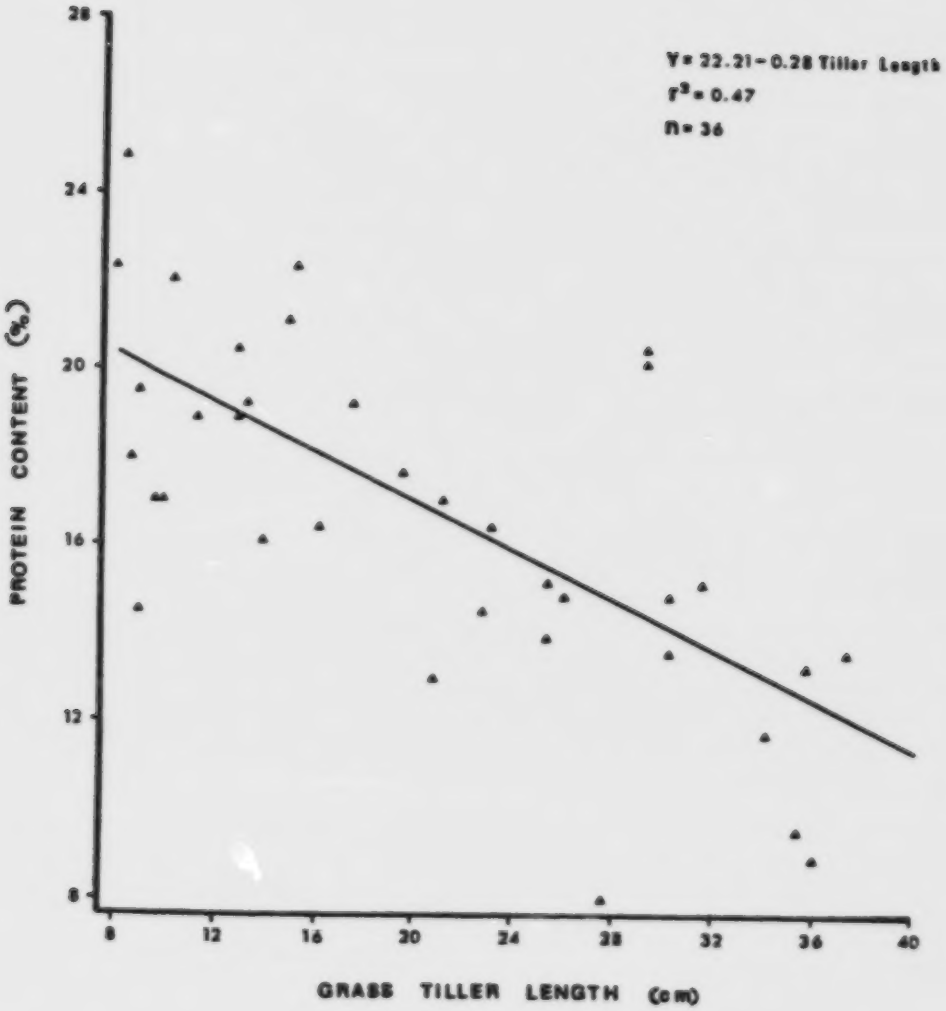

Figure 19. Relationship between tiller length and crude protein concentrations of new grasses on Stone's sheep ranges in northeastern British Columbia (1980-1982).

therefore, was more nutritious in the summer months. Fibre (ADF) (Figs. 13 and 16) was significantly lower ($P < 0.1$) at high elevations compared to subalpine slopes during July and August for forbs and from June-August in graminoids. Protein levels (Figs. 14 and 17) in July were significantly higher ($P < 0.1$) for both graminoids and forbs at high elevations compared to the subalpine. Lignin (Fig. 18) levels of forbs from high elevations were significantly lower ($P < 0.1$) than levels for subalpine forbs during July and August. Lignin levels in graminoids were extremely variable and difficult to interpret (Fig. 15). Although the quality of alpine forage tended to be superior to forage from the intermediate Spruce-Willow-Birch zone, these differences were not statistically significant. On the ranges that the sheep were using, protein levels of forbs were significantly higher ($P < 0.1$) than levels in graminoids in May and June. ADF levels of forbs were significantly lower ($P < 0.1$) than levels in graminoids from June to August.

The limited data on browse quality also show that the protein level of high elevation willows tended to be higher than the level in the poplar browse available at subalpine elevations (Table 5).

Data on *in vitro* dry matter digestibility (DMD) were too sparse to make valid comparisons (Table 4). Therefore, values for DMD were calculated based on values for protein and ADF levels using the equation: % DMD = 67.05 + 0.23 (% protein) - 0.66 (%ADF), which was calculated from the data and had $r^2 = 0.86$, S.E. = 3.5, n = 42. These calculated values are presented in Fig. 20. Although the differences were not statistically significant, the data suggest the same pattern of gradually declining forage quality throughout the growing season with high elevation forage being superior to subalpine forage in summer.

The differences in forage quality between ranges appeared to decline as fall approached and by winter there was no difference between alpine and subalpine forage.

FOOD HABITS

There are several problems which detract from the accuracy of the fecal fragment analysis data on food habits. The major problem is that differential digestibility of different plant species can result in the proportion of different plant species in the feces differing from the proportion in the diet. Some researchers have developed correction factors for

Table 5. Quality analysis of browse species on Stone's sheep ranges in spring and summer in northeastern British Columbia (1980-1982).

Source	Cell Contents %	ADF %	Lignin %	Protein %	In vitro DMD [b] %	n
June 5						
SWB Salix [a]	72.0	19.7	2.9	24.6	-	1
SWB Betula	80.6	13.0	1.7	25.4	-	1
SWB Arctostaphylos	80.7	7.1	3.1	16.5	-	1
June 25						
alpine Salix	78.1-79.0	15.8-16.7	5.0-5.3	23.9	46.4-60.6	2
SWB Salix	78.1	17.2	5.9-6.1	21.7-22.1	46.2-47.7	2
subalpine Populus	76.9-77.1	15.4-15.6	6.2	17.0-18.0	46.8	2
July 17						
alpine Salix	77.0	15.3	1.1	30.7	-	1
SWB Salix	73.7	8.2	2.2	16.2	-	1

[a] SWB= spruce-willow-birch zone

[b] DMD = dry matter digestibility

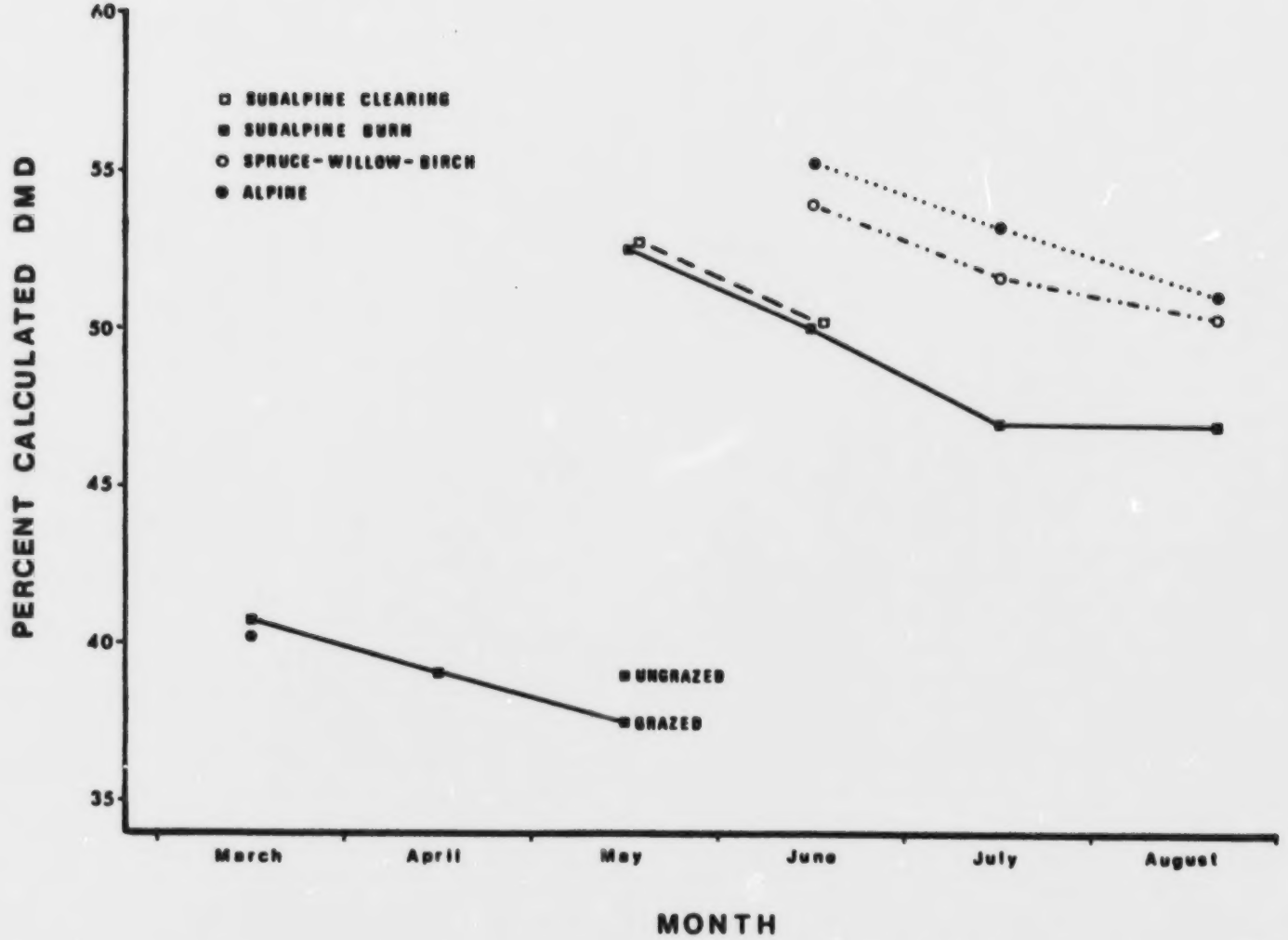

Figure 20. Calculated values for dry matter digestibility (DMD) of graminoids on different Stone's sheep ranges in northeastern British Columbia (1980-1982).

differential digestibilities of plant types but these values may not be accurate when extrapolated to an entirely new situation. Rumen analysis of food habits is more accurate because there is less opportunity for differential digestibility to alter the proportion of plant fragments. Comparison of food habits of the same animals by both rumen and fecal analysis (Tables 6 and 8) showed that although the results did not agree exactly, there was no consistent pattern to the deviation. For example, in three cases fecal analysis underestimated total grass and sedges compared to rumen analysis whereas in two other cases it overestimated total grass and sedges. Comparison of fecal analysis data from April 21, 1981 to data from two rumen samples collected at the same time showed that the fecal data tended to fall between the values from the two rumen analyses suggesting that the error in the fecal analysis technique was less than the variability in rumen samples from different animals.

Another problem was that the fecal analysis was based on one pooled sample from a certain collection period. Therefore, there was no measure of variance for the samples.

Given these problems, it would be unwise to put much significance on small differences (i.e., < 10%) in the data on food habits. Rather, I analysed the data looking for broad patterns in the food habits throughout the year.

Winter Food Habits

Sheep using alpine slopes in winter (February, March) were feeding heavily on sedges (Carex spp.) (Table 8; Fig. 21). In the February samples, blue grass (Poa spp.) was very important whereas in the March sample, lichen was very high in both the rumen and fecal samples. Overall, grasses and sedges made up most of the diet with forbs making up a smaller part and browse being quite unimportant.

Sheep using burned, subalpine slopes in winter were feeding primarily on rye grass (E. innovatus) and blue grass (Poa spp.) (Table 7). Forbs made up a smaller amount of the diet and browse and lichen were unimportant food items.

Spring Food Habits

The descent of sheep from alpine areas to subalpine clearings in April was evident in the decrease in sedges and lichen in the diet and the heavy use of subalpine grasses, particularly E. innovatus, and browse species

Table 6. Food habits of Stone's sheep on unburned range in northeastern British Columbia (1980-1982) determined by rumen analysis.

	March 23 1981 alpine	April 21 1981 subalpine	April 21 1981 subalpine	June 20 1981 alpine	June 25 1981 alpine
	%	%	%	%	%
Carex spp.	38.6	8.8	2.3	6.5	10.8
Elymus spp.	3.8	25.7	42.0	8.0	1.1
Poa spp.	12.2	8.8	8.3	19.7	19.5
Festuca spp.	0.6	0.4	1.6	0.0	0.0
TOTAL GRAMINOIDS	55.2	44.6	54.2	34.2	31.4
Oxytropis spp.	0.0	0.0	0.0	0.0	48.0
Lupinus spp.	0.0	1.4	7.8	18.0	2.7
Dryas spp.	0.0	0.0	1.0	0.0	0.0
Astragalus spp.	0.0	2.3	0.0	0.0	0.0
Other forbs	0.0	5.0	8.7	18.9	12.5
TOTAL FORBS	3.8	8.7	17.5	36.8	63.2
Conifers	0.6	2.6	0.2	0.0	0.0
Salix spp.	0.0	3.8	1.9	16.4	1.6
Vaccinium spp.	0.0	5.8	1.6	0.0	0.0
Rosa spp.	0.0	2.2	0.0	1.2	0.0
Populus spp.	0.0	3.8	3.8	0.0	0.0
Betula spp.	0.0	4.2	5.2	0.0	0.0
Other browse	0.0	0.0	0.0	9.4	3.7
TOTAL BROWSE	2.4	22.4	12.7	27.0	5.3
Lichen	38.6	9.0	12.8	1.8	0.1
Moss	0.0	15.3	2.8	0.0	0.0

Table 7. Food habits of Stone's sheep on subalpine burned range in northeastern British Columbia (1980-1982) determined by fecal analysis.

	February 24 1982	March 19 1981	April 6 1982	April 22 1982	May 7 1982	May 13 1981	May 18 1980	June 22 1980	November 1982
Carex spp.	7.7	9.0	12.6	7.7	7.2	13.0	0.6	1.3	3.8
Elymus spp.	29.6	13.9	26.3	19.3	23.3	46.5	-	-	31.8
Poa spp.	49.4	26.8	29.9	16.4	36.9	16.7	-	-	31.1
Agropyron spp.	0.0	3.6	0.0	4.4	0.0	4.0	-	-	0.0
Festuca spp.	0.0	3.1	0.0	2.3	0.0	3.7	-	-	0.0
Other grasses	0.0	0.0	0.9	0.0	3.2	0.0	-	-	0.0
TOTAL GRAMINOIDS	86.8	56.4	69.7	50.1	70.6	83.9	74.3	46.0	66.7
Artemesia spp.	-	0.0	-	0.0	-	0.0	-	-	12.2
Achillea spp.	-	0.0	-	30.4	-	0.0	-	-	0.0
Lupinus spp.	-	3.0	-	2.9	-	2.3	2.1	4.3	5.8
Dryas spp.	-	0.0	-	2.0	-	0.0	3.0	6.4	0.0
Astragalus spp.	-	12.3	-	0.0	-	2.0	-	-	0.0
Other forbs	-	14.7	-	3.0	-	7.4	-	-	5.5
TOTAL FORBS	13.3	30.0	26.9	37.3	29.4	11.7	14.6	27.0	23.5
Conifers	0.0	1.5	0.0	2.1	0.0	3.3	0.0	0.0	0.0
Other browse	0.0	2.9	3.4	5.0	0.0	0.4	10.3	23.0	0.0
TOTAL BROWSE	0.0	4.4	3.4	7.1	0.0	3.7	10.3	23.0	0.0
Lichen	0.0	9.2	0.0	5.5	0.0	0.7	0.8	3.0	0.0

A dash (-) indicates that the proportion of the food type is lumped with others for that group.

Table 8. Food habits of Stone's sheep on unburned range in northern British Columbia (1980-1982) determined by fecal analysis.

	February 1982	March 23 1981	April 21 1981	May 13 1982	May 18 1981	May 22 1982	May 28 1980	June 5 1981	June 20 1981	June 25 1982 rams	June 25 1982 ewes	July 3 1980	July 12 1981	August 1980
Carex spp.	35.0	37.0	5.4	3.7	10.4	8.5	12.9	12.8	22.4	12.5	7.9	30.6	27.4	6.0
Elymus spp.	6.3	5.3	33.6	23.0	25.9	21.8	-	0.0	0.0	0.0	2.0	-	0.5	-
Poa spp.	25.0	2.2	7.3	61.6	29.7	42.4	-	10.0	14.6	10.1	13.0	-	7.8	-
Festuca spp.	0.0	0.0	2.9	0.0	2.2	0.0	-	1.5	5.2	0.0	0.0	-	1.1	-
Other grasses	1.2	0.0	0.2	0.0	2.1	4.7	-	2.9	0.4	0.0	0.0	-	0.0	-
TOTAL GRAMINOIDS	67.5	44.8	49.4	88.3	70.3	77.4	63.4	27.2	42.6	22.6	22.9	48.3	36.8	53.6
Oxytropis spp.	0.0	0.0	0.0	0.0	0.0	5.9	-	0.0	0.0	24.9	45.9	-	0.0	-
Lupinus spp.	9.7	1.4	4.0	0.0	4.1	0.0	3.2	2.8	7.0	3.2	1.6	7.1	6.6	2.6
Dryas spp.	3.0	0.0	0.0	0.0	0.0	0.0	2.9	4.2	1.3	0.0	0.0	4.4	3.0	1.8
Astragalus spp.	7.1	0.0	0.0	0.0	0.0	0.0	-	11.8	3.4	3.9	1.0	-	10.5	-
Other forbs	4.9	6.3	7.1	8.0	7.7	6.9	13.4	4.0	2.2	34.1	16.9	18.5	4.1	19.2
TOTAL FORBS	24.7	7.7	11.1	8.0	11.8	12.8	19.5	22.8	13.9	66.1	65.4	30.0	24.2	23.6
Conifers	0.0	1.5	3.5	0.0	0.0	0.0	0.0	4.2	1.7	0.0	0.0	0.0	4.4	0.0
Salix spp.	0.0	1.8	2.0	0.0	0.0	0.0	-	17.8	17.7	8.1	5.5	-	14.6	-
Vaccinium spp.	0.0	1.8	2.0	0.0	0.0	0.0	-	7.7	6.5	0.0	0.0	-	4.8	-
Rosa spp.	0.0	1.0	3.2	0.0	1.9	0.0	-	0.0	1.7	0.0	0.0	-	1.5	-
Arctostaphylos spp.	0.0	1.1	2.3	0.0	2.2	0.0	-	2.0	2.1	0.0	0.0	-	2.5	-
Populus spp.	0.0	0.0	0.0	0.0	0.0	0.0	-	8.6	4.3	0.0	0.0	-	2.7	-
Other browse	0.9	1.9	4.0	1.5	4.0	4.5	-	6.2	8.5	1.0	3.0	-	4.1	-
TOTAL BROWSE	0.9	12.0	20.3	1.5	14.7	4.5	11.7	46.5	42.5	9.1	8.5	16.5	34.6	7.4
Lichen	6.9	35.5	15.6	2.2	3.2	5.3	5.4	3.5	1.0	2.2	3.2	5.2	3.4	15.4
Mosses	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0

A dash (-) indicates that the proportion of that food type is lumped with others for that group.

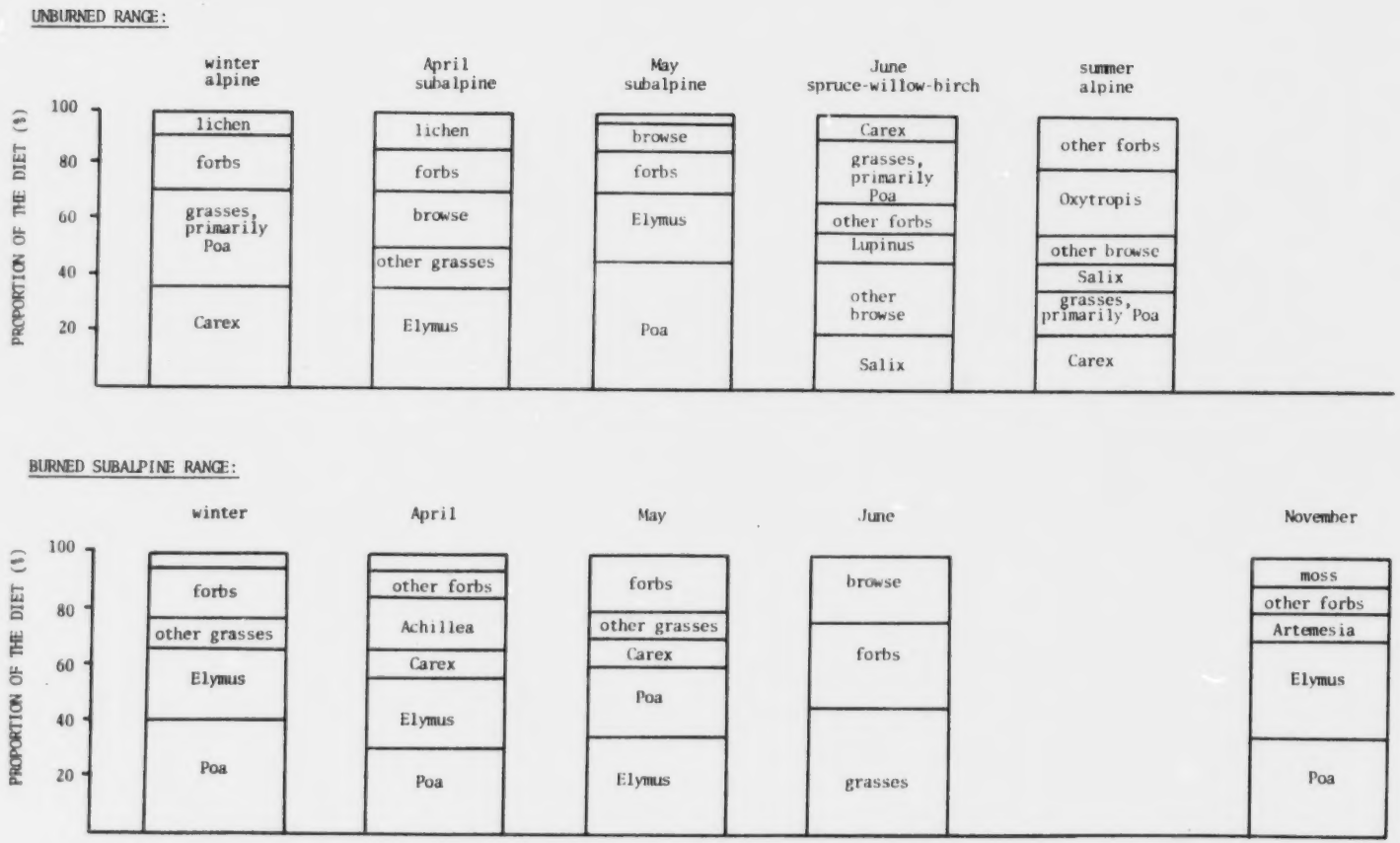

Figure 21. Summary of seasonal food habits for Stone's sheep determined by fecal analysis on burned and unburned ranges in northeastern British Columbia (1980-1982).

including conifers.

The onset of new spring growth resulted in the sheep feeding primarily on new grasses (E. innovatus and Poa spp.) throughout May on both burned and natural slopes. One sample (April 22, 1982) from the burned range indicated that the most important food was yarrow (Achillea spp.), a forb which began growing very early on the spring range.

Movement to higher elevations in June was associated with a decrease in grasses and an increase in forbs in the diet. Locoweed (Oxytropis spp.) was the single most important food item at this time. Heavy use of shrubs, especially willows, at this time corresponded to new leaf production on shrubs. Sheep were observed to browse extensively on willow at this time of the year. Poplars were used in early June but by late June the sheep had migrated above the upper altitudinal limit of poplars.

Summer Food Habits

Sedges were the most important food item of sheep on alpine summer range. In addition, a wide assortment of forb and browse species were also taken. Willows were a major food source and sheep were regularly observed browsing on willows at this time of year.

Fall Food Habits

Information on fall food habits is only available for sheep using burned, subalpine range. Grasses (Poa spp. and E. innovatus) made up the bulk of the diet but forbs, particularly Artemisia spp. were also eaten.

NUTRITIONAL INDICES OF THE SHEEP

The sample variance for fecal protein values could be greatly reduced by correcting for the ash content of the feces, that is, calculating the protein content of the non-ash portion of the feces. This correction was particularly important in samples collected near mineral licks in which feces often contained up to 88% mineral material and averaged up to 45% (Table 9). Samples with high ash content had abnormally low protein content compared to other samples; correcting for ash content resulted in a much lower variability in the samples. For example, in a group of samples in which ash content varied from 14-47%, correcting for the ash content reduced the standard deviation of the fecal protein values from 5.46 to 3.46. Therefore, unless otherwise stated, all further

Table 9. Seasonal changes in fecal ash content of Stone's sheep on burned and unburned ranges in northeastern British Columbia (1980-1982).

Date	Delano/Yedhe area ($\bar{X} \pm SD$)	n	Toad Mountain area ($\bar{X} \pm SD$)	n
	%		%	
February	15.8 ± 3.5	13	12.1 ± 0.9	8
March	-		15.5 ± 5.5	11
early April	-		14.6 ± 3.0	14
late April	-		16.9 ± 4.6	8
early May	10.3 ± 1.6	12	16.4 ± 7.2	12
late May	13.8 ± 1.3 20.2 ± 10.3[a]	5 9	16.9 ± 2.1	5
early June	23.8 ± 13.5[a]	16	45.9 ± 14.9	3
late June	22.6 ± 4.7[a]	20	21.9 ± 10.0	4
early July	33.6 ± 21.1[a]	10	-	
late August	14.2 ± 2.2[a]	5	21.0 ± 8.9	3
November	-		15.5 ± 5.6	7

[a] samples collected at a mineral lick.

discussion of fecal protein levels refer to values corrected for ash.

Fig. 22 shows the fecal protein values for sheep in the Yedhe/Delano area compared to sheep in the Toad River area. Lowest values (10-12%) occurred in winter with a dramatic increase during green-up in May. Peak values (30%) were attained on alpine range in late June and then gradually decreased throughout the autumn reaching low winter values by November. Fecal protein values for sheep on alpine range in February were significantly greater ($P < 0.05$) than values for sheep on the subalpine burned range of Fertilizer Mountain. This observation was surprising because the alpine range contained almost no food compared to the subalpine range. Fecal protein values from February of 1982 when the sheep were restricted to a small, heavily grazed area of the total range were not different from winter values of 1981 when the entire range was being used. Similarly the values from April 1982, when large areas of previously unavailable range became available because of snow melt, were not significantly different from the February values when the sheep were concentrated in a small area. The latter two points are contrary to the hypothesis that heavy grazing results in a decrease in the quality of food intake by the sheep.

During May, although fecal protein values of sheep increased dramatically on both burned and unburned range, it appeared that the increase was 7-10 days earlier for sheep on burned range. Values for sheep in the Yedhe valley on May 20, 1982 were significantly less ($P < 0.05$) than the values for sheep on Fertilizer Mountain two days earlier which demonstrates that fecal protein values on unburned range lagged behind values for sheep on burned range. Fecal nitrogen values throughout the summer were similar in both populations which was not surprising because both populations were utilizing similar alpine habitat at that time of the year.

DAPA values (Fig. 23) showed similar patterns and relationships to fecal protein but lack of replicates precluded statistical analysis.

FOOD SELECTIVITY

Selection Of Species

There was a large amount of variance in both the estimates of food availability and food habits which made any analysis of plant species selection difficult.

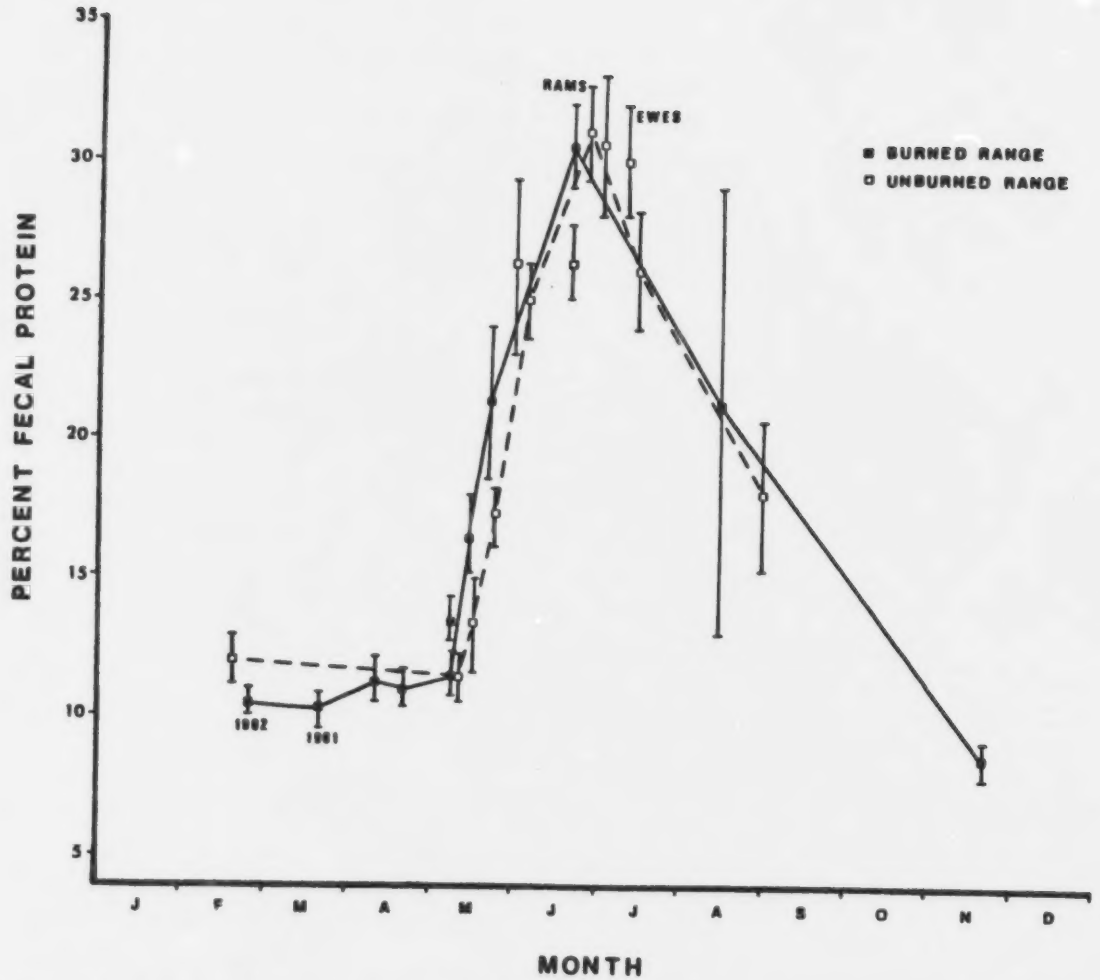

Figure 22. Seasonal pattern of fecal protein levels (corrected for ash content) for Stone's sheep on burned and unburned ranges ($\bar{X}$ ± 95% C.I.) in northeastern British Columbia (1980-1982).

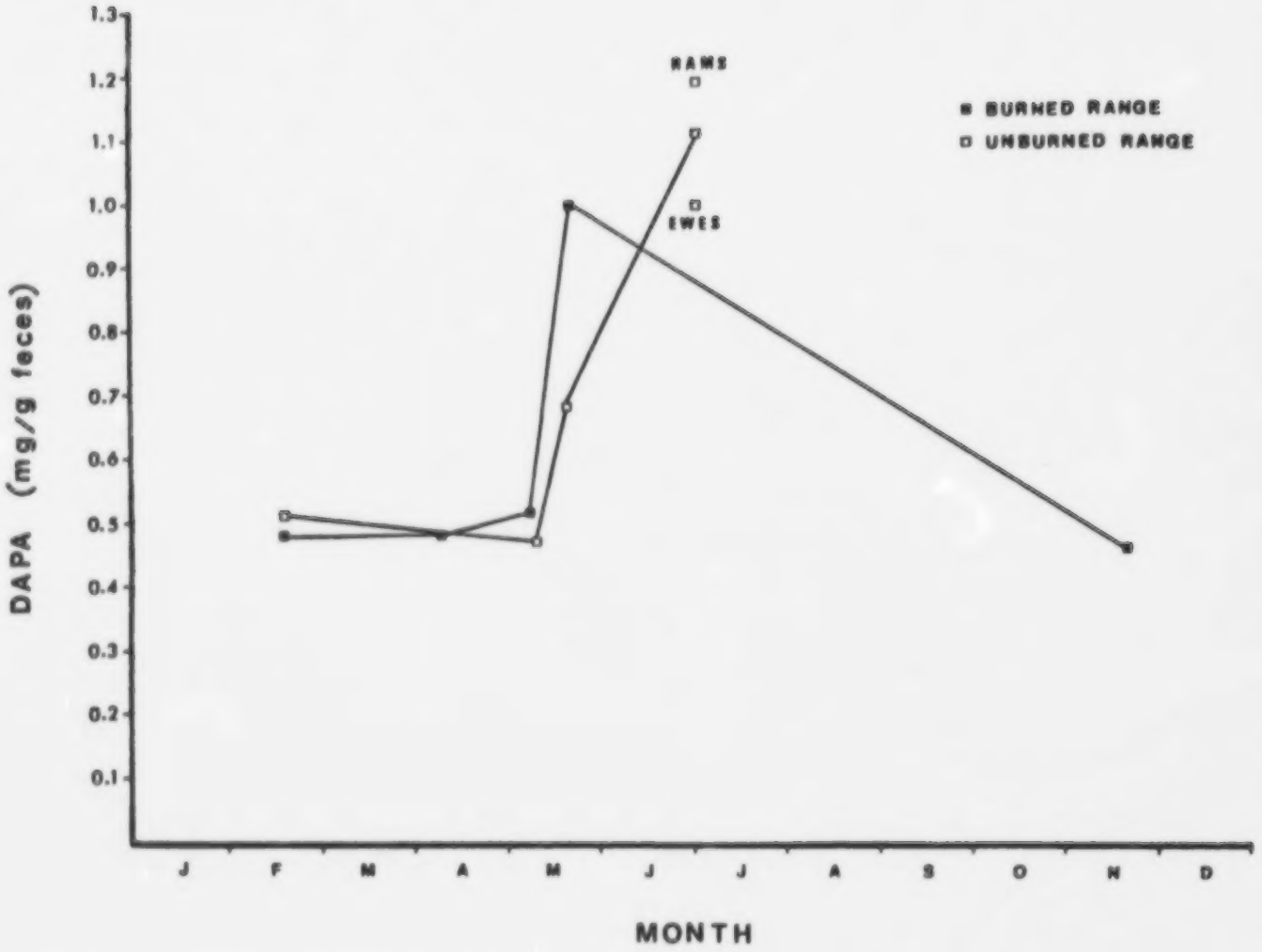

Figure 23. Seasonal pattern of DAPA concentrations for Stone's sheep on burned and unburned ranges in northeastern British Columbia (1980-1982).

Therefore, I restricted the analysis to major differences between use and availability.

1. Species Selected Against

Lichens covered up to 30% of alpine ranges (Table 3) and in winter they sometimes became the only vegetation on alpine ranges. However, they usually comprised only a very small proportion of the diet (about 5%). This small amount could have been consumed accidentally while feeding on sedges and forbs tangled in lichen. Dryas integrifolia and Arctostaphylos uva-ursi were the dominant ground cover plants on alpine and subalpine areas respectively (Tables 2 and 3). However, they were only found in trace amounts in the diet (< 5%).

Sheep were not always on ranges with access to conifers but in spring when they were, conifers were not extensively used even though they were essentially unlimited to any sheep which chose to feed on them.

Betula glandulosa was about as abundant as willows on the range in June but was not eaten whereas willows were heavily used at this time (Table 8).

Lupinus arcticus was a common food (Table 8) but the proportion in the diet was far less than its availability on alpine ranges (usually 50-80% of forb biomass).

2. Species Selected For

The only species which appeared to be heavily selected for year-round were Poa spp. which were an important food on subalpine and alpine ranges (Fig. 21) even though it was sparsely distributed. At particular times of the spring and summer, various forb species including Achillea spp. and Oxytropis spp. were taken far in excess of their availability.

Selection Of Graminoids Versus Forbs

Selection for graminoids versus forbs did not differ from availability on spring ranges (Table 10). There appeared to be selection against forbs in favour of graminoids on alpine range in summer.

Selection Of Superior Quality Food

The protein content of the food intake was calculated based on the protein content of grasses, forbs, and browse and the proportion of these items in the diet based on the fecal analyses data (Fig. 24). Fecal protein values

Table 10. Proportion of forbs versus graminoids in the diet of Stone's sheep compared to availability on the range.

	Proportion of Diet (%)		Availability (g/m^2)	
	Graminoids	Forbs	Graminoids	Forbs
Burned subalpine, May	70	15	20	5
	(4.7	1)	(4	1)
Alpine, June-July	45	30	5	10
	(1.5	1)	(0.5	1)

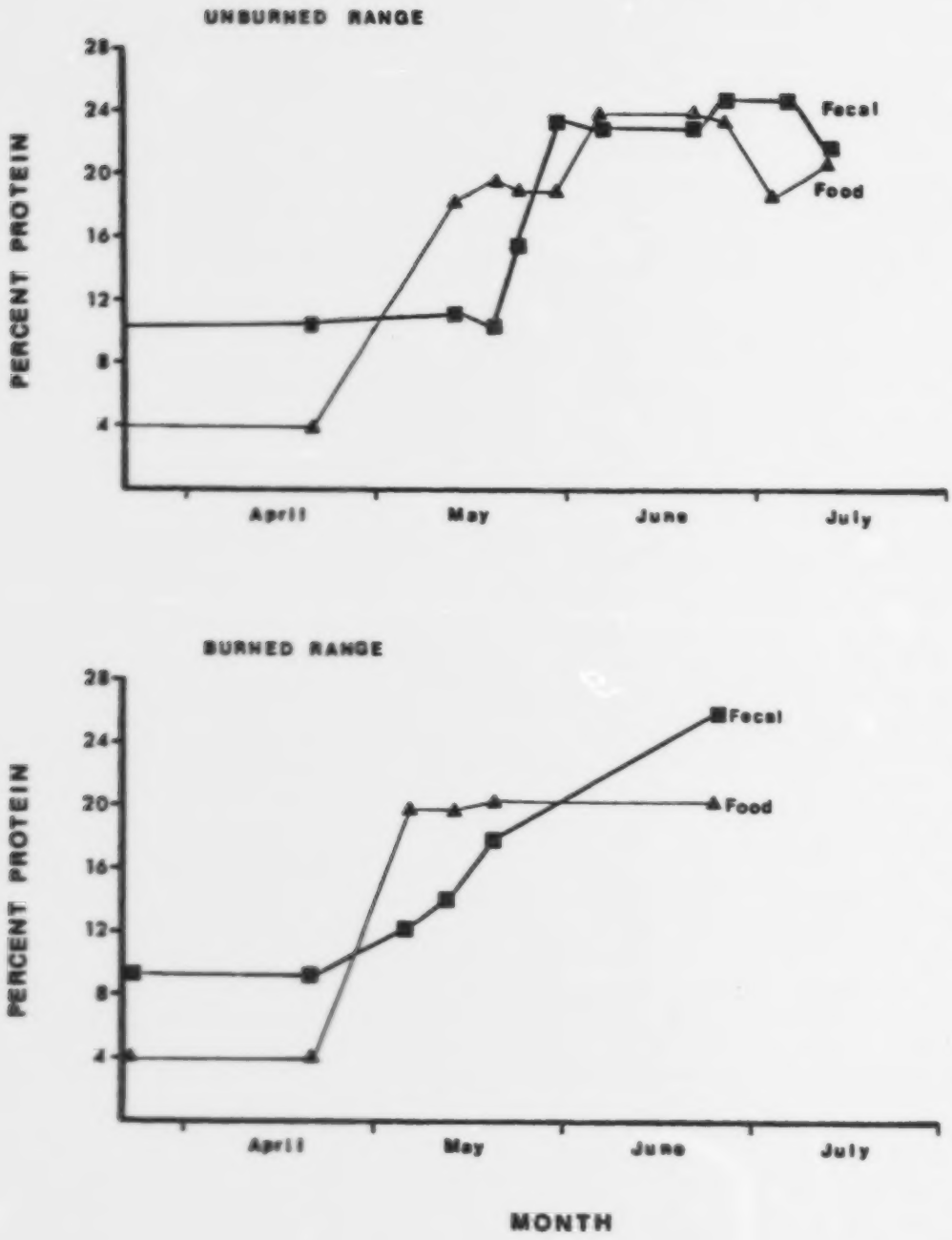

Figure 24. Relationship between protein concentrations of the available forage and the fecal protein concentrations of Stone's sheep (standardized to 15% ash content).

(uncorrected for ash) have an almost 1:1 relationship to crude protein in the diet of mountain sheep (Hebert 1973). Fecal protein values (corrected for ash) were reduced by 15% to make them comparable to the uncorrected fecal protein levels in Hebert's study because the ash level in the feces of sheep not using licks is about 15% (Table 9). These values were compared with the estimated protein content of the food in Fig. 24. Fecal protein values were higher than forage protein values when the animals were feeding on winter vegetation. In spring, the increase in fecal protein values lagged behind the increase in food quality by about 10 days. By summer, fecal protein values were similar to the estimated food protein levels.

If sheep were being highly selective for more nutritious parts of the forage, the fecal protein values should have been higher than the protein values of forage samples collected at random. The data did not appear to support this hypothesis. The food intake of the sheep did not appear to be any higher in protein than the average food available to them on the range.

MINERAL NUTRITION

Soil Mineral Concentrations

Soil mineral concentrations are presented in Table 11. Total nitrogen concentrations were lower in the two talus slope areas (Yedhe, Delano) than in the soils from the more stable areas. These talus slopes were used as spring range by sheep in these two areas. The carbon:nitrogen ratios in all the soils were low enough to ensure that a net gain in nitrogen mineralization was occurring (Thompson and Troeh 1978). However soil nitrate concentrations were undetectable (< 1 ppm). The abundance of nitrogen-fixing plants in the area (Shepherdia spp., Lupinus spp., Oxytropis spp., Astragalus spp., and other legumes) also indicated a soil deficient in available nitrogen even though total nitrogen concentrations were reasonably high. The low nitrate concentrations may result from low rates of nitrification characteristic of cold, subarctic soils (Mitchell and Offner 1982).

Phosphorous concentrations were extremely low in all soils except for Fertilizer Mountain. Otherwise, all the other nutrient concentrations (Ca, Mg, K) were not likely to be severely limiting to plant growth (T. Ballard, pers. comm.). The major soil nutrient concentrations (N, P, K) tended to be higher on Fertilizer Mountain than from other sites which suggested that the frequent burning in this area had no detrimental effect on soil nutrients and

Table 11. Mineral concentrations and pH of soils and mineral licks in the Toad River area.

	pH	total N %	C %	C:N	P ppm	Ca ppm	Mg ppm	K ppm	Na ppm	S ppm
Yedhe	7.5	0.10	1.17	11.7	u	3026	73.0	39.0	u	-
Delano	6.0	0.08	1.43	17.9	u	1202	145.9	78.o	u	-
Tower	6.2	0.44	1.81	4.1	u	2645	340.5	78.0	u	-
Magnum	7.0	0.89	16.25	18.3	2.1	8958	681.0	78.0	u	-
Fertilizer	6.8	0.52	3.23	6.2	16.6±3.1[a]	3968	425.6	117.3	u	7.5±1.2[a]
$\bar{X} \pm$ SD	6.7±0.6	0.4±0.3	4.8±6.5	11.6±6.5	-	3959±2965	333±241	78.0±27.6	u	-
Mineral Licks:										
Churchill Mine	8.1	0.01	0.10	10.0	u	3387	133.8	117.3	92.0	-
Toad Bridge	8.8	0.08	0.72	9.0	u	3447	1252.4	39.0	23.0	-
Toad Mountain	7.6	0.12	0.67	5.6	u	4329	389.1	39.0	23.0	-
$\bar{X} \pm$ SD	8.2±0.6	0.1±0.06	0.5±0.3	8.2±2.3	u	3721±527	592±586	65±45	46±40	-

[a] $\bar{X} \pm$ SD, n=8

u = undetectible, less than 0.1 ppm for phosphorus and less than 23.0 ppm for sodium.

may even have been beneficial.

Forage Mineral Concentrations

Forage mineral concentrations are compared to the mineral requirements of domestic sheep (NRC 1975; Maynard et al. 1979) in Table 12. These values are for maintaining sheep in good condition and probably exceed the needs for basic survival. Winter forage was deficient in nitrogen, phosphorous, potassium, zinc, and possibly copper. Sulphur levels were low but probably adequate considering the low nitrogen intake at this time. Levels of calcium, magnesium, iron, and manganese were adequate to meet the requirements of sheep. Levels of the five deficient minerals, particularly potassium, tended to be higher in the subalpine winter forage than the alpine forage but the data are too scant for statistical comparisons.

New spring grasses from all sites met or came quite close to sheep requirements for all minerals (Delano was slightly low in zinc and sulphur). The calcium: phosphorous ratio was also close to the optimum of 2:1. Similarly, summer grasses and sedges contained adequate levels of all minerals except phosphorous. The sedges from Magnum Valley with the high copper levels in July were collected adjacent to the abandoned copper mine. Summer willow leaves contained mineral levels exceeding sheep requirements for all minerals.

Behaviour At Mineral Licks

Use of mineral licks by sheep occurred primarily from April to July but use of a lick in November was also observed. Deep snow prevented the sheep from using many of the sites, including the Churchill Mine, during much of the winter until late May. Sheep were often observed quickly approaching a lick from several kilometres away in a manner which suggested a strong determination to get to the lick. At the lick the animals became obsessed with licking and exhibited a reduced level of caution, often allowing people to approach within 2-3 metres before moving away. The sheep either licked the ground with their tongue or took in a mouthful of soil and chewed it. The intensity of mineral lick use during the summer was reflected in the fact that the feces of some sheep during this time contained up to 88% mineral material and averaged up to 45% (Table 9). Individual sheep usually spent from 1-4 hours licking before moving off to feed or rest. Most licking took place during mid-day. There were usually no sheep at the Churchill Mine early in the morning but they began to move in about 0800h and left the

Table 12. Mineral concentration in forages from Stone's sheep ranges in northeastern British Columbia (1980-1982) compared to requirements of domestic sheep.

	N %	P %	Ca %	Mg %	K %	Fe ppm	Zn ppm	Mn ppm	Al ppm	Cu ppm	B ppm	S %
Subalpine winter forage:												
Fertilizer Mountain	0.73	0.09	0.83	0.11	0.43	63.0	17.0	24.0	50.0	3.0	7.64	0.11
Toad Mountain	0.58	0.07	0.83	0.75	0.54	28.0	18.0	5.0	20.0	6.0	7.52	0.09
Alpine winter forage:												
Delano	0.40	0.04	0.73	0.90	0.18	63.0	5.0	74.0	60.0	1.0	5.70	0.09
Toad	0.52	0.06	0.70	0.85	0.12	43.0	11.0	16.0	30.0	1.0	5.20	0.09
Magnum	0.58	0.03	0.71	0.95	0.09	64.0	9.0	38.0	60.0	1.0	5.40	0.10
Mean	0.50	0.04	0.71	0.90	0.13	56.7	8.3	42.7	30.0	1.0	5.40	0.90
Subalpine spring range:												
Delano	3.43	0.27	0.77	0.13	-	119.0	15.0	43.0	190.0	8.0	5.50	0.11
Fertilizer Mountain	2.92	0.31	0.46	0.13	2.45	112.0	35.0	49.0	130.0	6.0	7.80	0.21
Magnum	3.50	0.27	0.50	0.17	2.78	140.0	61.0	37.0	190.0	8.0	4.80	0.24
Mean	3.28	0.28	0.58	0.14	2.62	123.0	37.0	43.0	170.0	7.3	6.00	0.19
Alpine range (July):												
Magnum Creek	2.50	0.20	0.47	0.17	1.76	160.0	55.0	34.0	60.0	111.0	8.80	0.22
Tower Mountain	2.40	0.18	0.34	0.17	1.96	60.0	26.0	61.0	10.0	2.0	6.40	0.21
Subalpine range (July):												
Fertilizer Mountain	1.90	0.23	0.43	0.11	2.60	48.0	25.0	20.0	10.0	4.0	4.10	0.15
Yedhe Creek	2.30	0.14	0.48	0.15	2.65	37.0	11.0	36.0	10.0	4.0	4.40	0.18
Delano	2.20	0.17	0.30	0.12	3.55	46.0	9.0	53.0	20.0	6.0	4.70	0.17
Mean	2.13	0.18	0.40	0.13	2.93	43.7	15.0	36.3	13.3	4.7	4.40	0.17
Alpine Salix (June)	3.60	0.31	0.75	0.30	1.43	188.0	101.0	31.0	333.0	8.0	20.00	0.30
SHEEP REQUIREMENTS:	1.60	0.25	0.25-0.50	0.06	0.50	25-40	20-30	16-40	0.0	5.0	0.0	0.18

area by 1800h. The frequency of use of licks by individual sheep is not well known but of 6 collared sheep using the Churchill lick, frequency of use by known individuals ranged from 1 to 6 days out of a 10-day observation period or an average use of once every 2-3 days. Sightings of sheep in subalpine areas during the summer were usually related to the animals using subalpine mineral licks. Sheep were observed moving quickly down from alpine areas to use the lick on Toad Mountain and at Mile 475 of the Alaska Highway but they then returned to alpine areas.

Mineral Licks

Many different forms of mineral licks were utilized in the area including: soil licks exposed along creek beds and road cuts; weathered, rocky outcrops; and, man-made sources, particularly the Churchill copper mine site and mill site. On Toad Mountain the sheep have created a small cave extending about 1.5 m into the side of the mountain by eating the soil.

Soil from mineral licks (Table 11) had lower total nitrogen and carbon levels than other soils in the area due to the lack of organic matter. The higher pH is the expected value for calcium carbonate mineral material without the acidifying effects of organic acids present in other soils. Levels of phosphorous, calcium, magnesium, and potassium were not different from other soil samples from the area. Soil levels of these elements were lower than the levels found in forage samples. Sodium was the only element which was higher in mineral lick samples which suggests that it was the mineral attracting sheep to these areas . Sodium was undetectable (< 23 ppm) in all the samples except for the three mineral lick samples. The sheep also became frantic in their efforts to get access to the salt blocks we used as bait for trapping indicating a strong drive to obtain sodium.

FORAGING BEHAVIOUR

Biting Rate

1. Daily Pattern

On the 2 occasions in April 1982 when the biting rate of individual ewes was observed throughout the daylight hours, there was no trend in the biting rate either throughout the day or during individual foraging bouts. Therefore, I concluded that it was not necessary to conduct day-long observations but rather a sample at any

time of the day would be representative of the biting rate throughout the day.

2. Sex and Age Differences

On the one day when the biting rate of rams and yearlings was determined, there was no significant difference ($P < 0.05$) between the biting rate of rams (30 ± 1.8 (S.E.) bites/minute), yearlings (30 ± 1.2 (S.E.) bites/minute), and ewes (34.2 ± 2.4 (S.E.) bites/minute) feeding on the same range.

3. Seasonal Pattern

The biting rate remained relatively constant throughout the spring-summer season under a wide variety of range types and forage distributions (Table 13). There was no difference between the biting rate of sheep on burned versus natural subalpine spring range. Overall it appeared that Stone's sheep maintained a relatively constant biting rate averaging about 30-35 bites/minute and that this rate was not obviously affected by the range characteristics.

Foraging Time

The proportion of daylight hours spent foraging remained constant throughout the winter-spring period for both ewe/yearling groups and ram groups (Tables 14 and 15). On average, ewe/yearling groups spent about 13% more of the daylight hours foraging than did rams. Also the proportion of time spent foraging was more variable from day to day for rams than for ewes/yearlings. The one atypical day of ewe/yearling activity (May 19) when foraging time was only 50% may have been due to a preponderance of yearlings on that day (6 yearlings, 2 ewes). This distortion was caused by adult ewes moving from the main slope to lambing cliffs at this time of year. These data represent a wide range of conditions including cratering through the snow in February, snow-free slopes with dead grass in March-April and new production in May. Similarly, there was no difference in proportion of time spent foraging between sheep feeding on subalpine burned range and sheep feeding on a natural subalpine clearing in May.

The proportion of daylight hours spent foraging remained constant even though the amount of daylight almost doubled from February to May. It appeared that in the winter the sheep were not foraging during darkness because the sheep were usually seen bedding down in the evening and were often seen bedding in the same spot the

Table 13. Biting rate of Stone's sheep ewes under different range characteristics (April-June).

Date	Biting Rate ($\bar{X} \pm SE$)	Number of observations [a]	Range Type	Forage Biomass (g/m^2)	Grass Tiller Length cm
April 9	35.0 ± 1.2	44	subalpine burn	162 dead	-
April 20	26.0 ± 0.6	90	subalpine burn	162 dead trace live	-
May 5	28.0 ± 1.0	22	subalpine burn	14 live grass	8
May 11	29.4 ± 1.2	35	subalpine burn	14 live grass	9
May 13	34.8 ± 2.6	11	subalpine clearing	1.5 live grass	10
May 20	34.2 ± 1.5	24	subalpine burn	20 live grass	13
May 22	34.8 ± 1.7	12	subalpine clearing	1.6 live grass	11
May 24	31.8 ± 2.2	11	subalpine burn	34.2 grass 15.4 forbs	13
June 28	37.7 ± 1.2	15	alpine	3.7 sedges 13.5 forbs	12

[a] 1 observation equals a 1-2 minute period of observation.

Table 14. Time budget and calculated bites/day for Stone's sheep ewes and yearlings (February-May).

Date	Number of observations	Percentage of daylight time				Observation period (hours)	Daylight hours foraging	Estimated bites/day
		Resting	Travelling	Foraging	Standing			
Senescent forage								
Feb. 8	1907	17.5	2.7	62.6	17.7	10	6.2	9600
Feb. 14	1767	21.0	2.0	67.0	10.0	10	6.7	10375
March 16	1965	32.0	2.0	62.0	4.0	12	7.4	13480
March 17	1807	21.0	5.0	67.0	6.0	12	8.0	14573
March 18	1677	21.0	7.0	69.0	4.0	12	8.2	14940
March 24	2341	24.0	4.0	70.0	3.0	13	9.1	16580
March 31	1696	27.0	1.0	64.0	8.0	13	8.3	15123
April 4	1744	34.0	2.0	60.0	4.0	14	8.4	15305
April 20	70	30.0	5.0	61.0	4.0	14	8.5	15487
May 5	2859	26.0	4.0	64.0	5.0	16	10.2	18584
New production								
May 7	954	29.0	4.0	61.0	6.0	17	10.4	18950
May 10	2322	30.0	3.0	63.0	5.0	18	11.3	20590
May 12	1925	25.0	6.0	60.0	9.0	18	10.8	19675
May 12[a]	918	30.0	1.0	63.0	5.0	18	11.3	20590
May 19[b]	1465	42.0	2.0	50.0	6.0	18	9.0	16400
May 25	935	32.0	1.0	64.0	3.0	18	11.5	20955
Mean		26.6	3.3	63.8	6.3			
Standard Deviation		4.4	1.9	3.1	3.8			

[a] sheep on natural subalpine clearing, all other data are for sheep on subalpine burned range.
[b] predominately yearlings.

Table 15. Time budget and calculated bites/day for Stone's sheep rams (February-May).

Date	Number of observations	Percentage of daylight time				Observation period	Daylight hours foraging	Estimated bites/day
		Resting	Travelling	Foraging	Standing			
Senescent forage								
Feb. 8	410	34.6	2.8	40.0	21.2	10	4.0	6195
Feb. 14	547	41.0	2.0	56.0	1.0	10	5.6	8673
Feb. 16	204	56.0	5.0	37.0	3.0	12	4.4	6814
Feb. 17	298	34.0	6.0	46.0	14.0	12	5.5	8518
April 4	505	42.0	1.0	49.0	8.0	14	6.9	12572
May 5	1586	28.0	4.0	58.0	10.0	16	9.3	16945
New production								
May 9	401	42.0	4.0	49.0	5.0	18	8.8	16035
May 10	2150	38.0	1.0	56.0	5.0	18	10.1	18402
May 12 [a]	362	34.5	2.5	56.9	6.0	18	10.2	18584
May 12	1885	38.0	3.0	54.0	4.0	18	9.7	17675
May 19	231	38.0	2.0	53.0	7.0	18	9.5	17300
May 19	248	35.0	4.0	58.0	3.0	18	10.4	18950
May 25	1461	39.0	4.0	50.0	7.0	18	9.0	16400
Mean		38.0	3.2	51.0	7.3			
Standard Deviation		6.7	1.5	6.8	5.4			

[a] sheep on natural subalpine clearing. All other data are for sheep on subalpine burned range.

following morning. In fact, in winter the sheep often remained bedded down for up to an hour after light was adequate to begin observations. Thus the observation period during winter included all or most of the total time spent foraging. In spring, the observation period did not include the entire day's foraging activity since most of the sheep usually began foraging before light was adequate to see them. Although most sheep usually had bedded down before darkness prevented further observation some foraging still continued beyond the observation period. The occurrence of a major foraging bout at dawn and dusk in conjunction with bedding activity at dusk suggested that extensive foraging did not occur during the several hours of darkness in the spring. Thus, the observation period definitely did not include the entire foraging period in spring but probably came close if in fact foraging did not occur during the peak of darkness. The time spent foraging for ewe/yearling groups went from 6.2 hours in February to 12+ hours in May and for rams went from 4-5 hours in February to 10+ hours in May.

Not all of the foraging time was spent actively feeding, particularly in winter when much of the foraging period was spent digging through snow to reach the food. The amount of time spent digging was dependent on the snow depth (Fig. 25) and averaged 15 - 20% during February 1982. In addition, throughout the year only 92% of the foraging time was spent actively feeding with the remaining 8% of the time spent searching, chewing, etc. This value is based on the difference between foraging time and active biting time determined during biting rate observations (n = 264).

The numbers of bites/day in Tables 14 and 15 were calculated by reducing the foraging time in February by 15% to account for cratering and then reducing all values of foraging time by an additional 8% to account for non-feeding time. The resultant values for feeding time was then multiplied by the average biting rate of 33 bites/minute.

Length And Number Of Foraging Bouts

Detailed day-long observations of two ewes in April showed that both animals had four foraging bouts throughout the day ranging from 60 minutes to greater than 240 minutes separated by rest periods ranging from 40 to 150 minutes. In both animals, the first foraging bout began before daylight and the last foraging bout continued into the darkness. Therefore, the exact duration of these bouts is unknown. In both cases, the longest foraging bout of the day (160+ and 240+ minutes) was the one

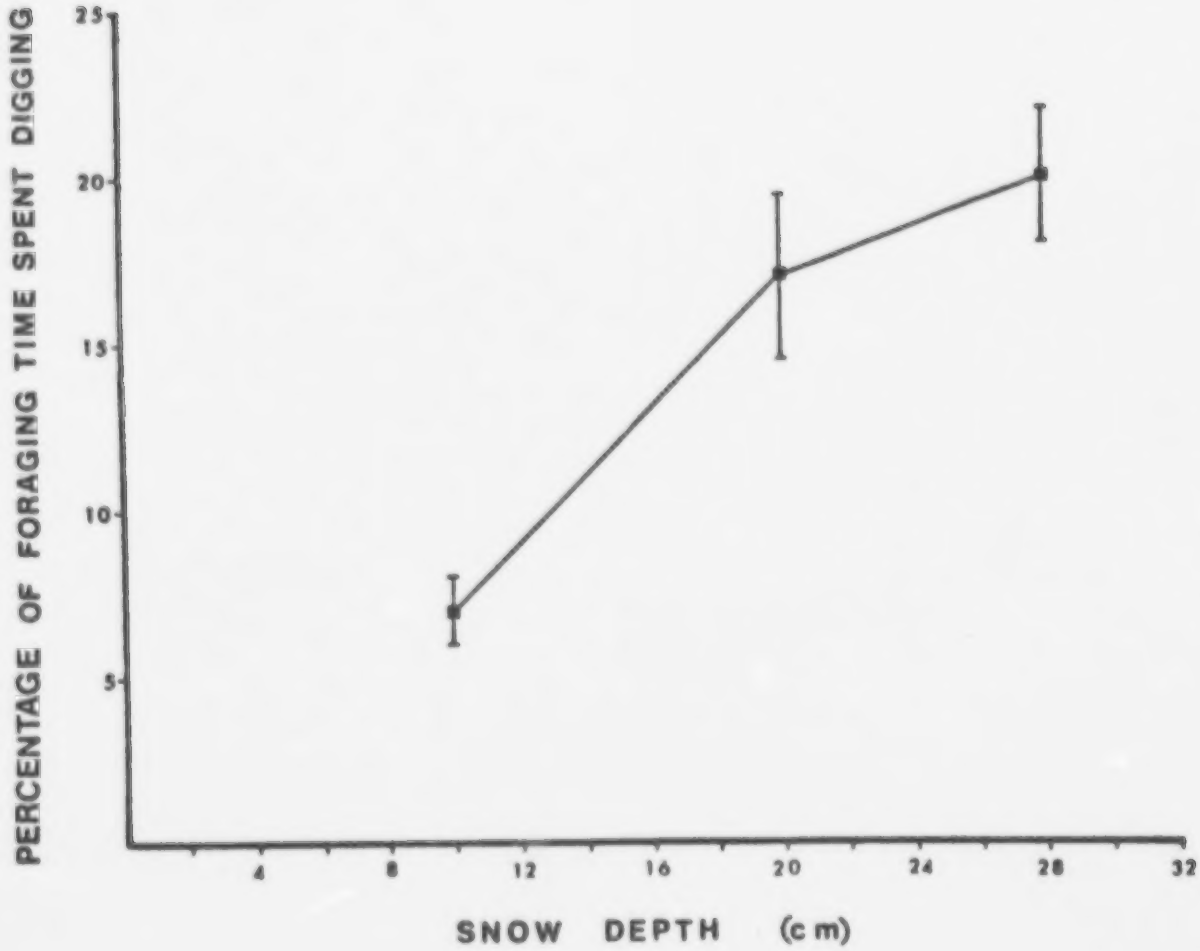

Figure 25. Relationship between snow depth and percentage of foraging time spent digging ($\bar{X} \pm$ standard deviation) by Stone's sheep.

preceding darkness.

The time budget data lumped for ewes/yearlings and for rams showed a similar pattern of four foraging bouts/day throughout May (Fig. 26). However, in February and March, the animals only had three foraging bouts/day. Both times of the year showed major dawn and dusk feeding bouts with the difference being the number of intervening bouts.

The fact that the pattern is quite distinct even in the aggregated data demonstrates that there was a great deal of synchrony in the behaviour of animals within a foraging group. However, it can also be seen from Fig. 26 that behaviour of rams compared to ewes/yearlings was often asynchronous (e.g., rams feeding while the ewes/yearlings were resting).

PARASITOLOGY

Lungworm larvae counts for winter and spring fecal samples are presented in Table 16.

Most larvae belonged to Protostrongylus spp. but in addition some samples contained up to 33 larvae/gram of dorsal-spined larvae, most likely Muellerius spp. (W. Samuel, pers. comm.). Lungworm counts from sheep using unburned range (Delano) were higher than samples from burned subalpine range in both winter and spring. However, the high spring count for the Delano samples probably resulted from a build-up occurring on the alpine winter range rather than reflecting on the quality of the spring range. In both areas, the spring counts were higher than the winter counts indicating that parasite loads continued to build up throughout the winter.

HORN GROWTH OF RAMS

The maximum increment in ram horn length occurred during the second year of life (annulus 1-2) and subsequently declined with age (Fig. 27). Horn growth of rams with access to burned range was significantly greater ($P < 0.05$) than on unburned range for yearlings but there was no difference for older ages. Despite this difference in yearling growth, there was no significant difference in total horn length between rams with access to burned range compared to unburned range (Fig. 28). The loss of the early horn growth advantage by sheep from burned range appeared to result from an increased rate of brooming (amount broomed is estimated by recorder on reporting form) in these animals (58.5 mm ± 12.3 (S.E.)) compared to

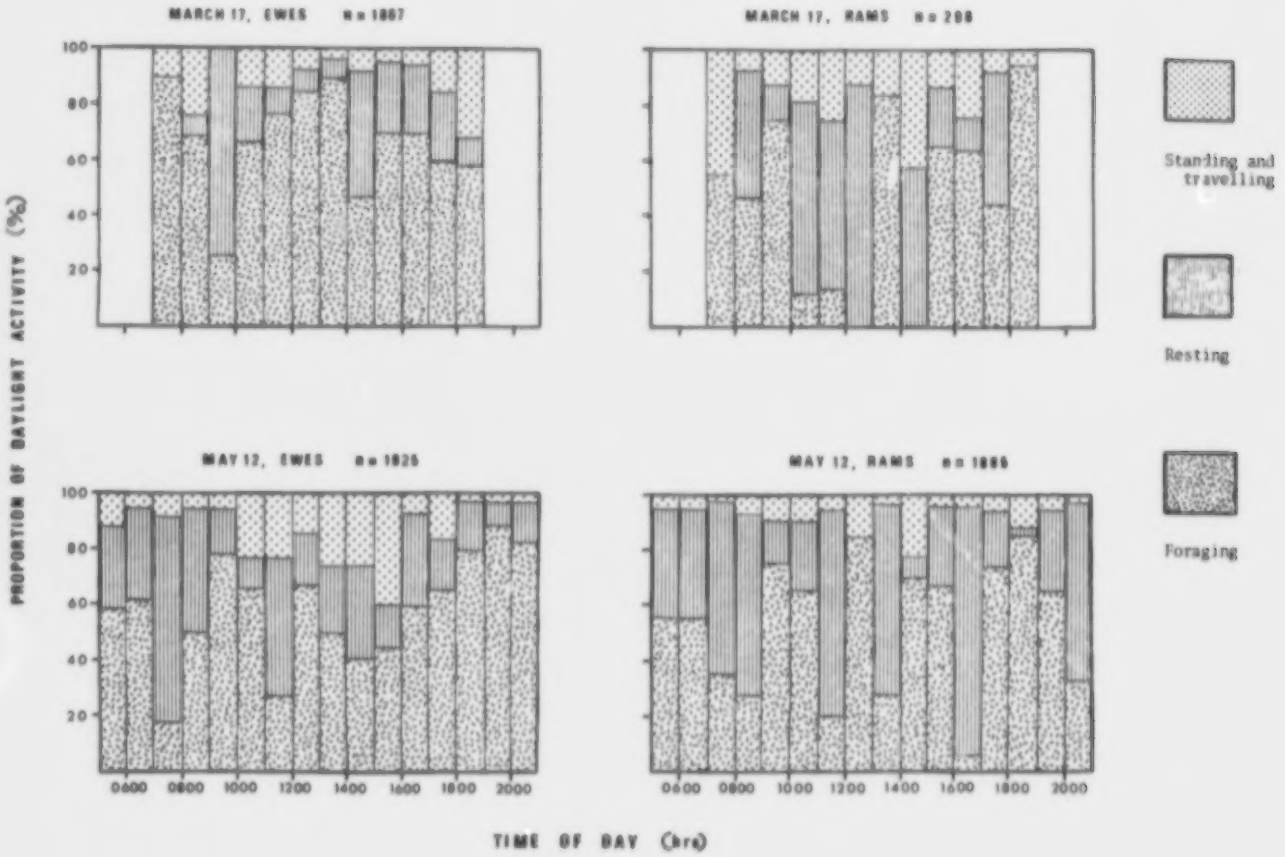

Figure 26. Typical daily time budgets of Stone's sheep ram groups compared to ewe/yearling groups in March and May.

Table 16. *Protostrongylus* larvae counts in feces of Stone's sheep on burned and unburned range in northeastern British Columbia (1982).

Location and Season	Number of larvae/g feces			
	$\bar{X}$	SE	range	n
Delano alpine, February	417	171	34-992	5
Fertilizer subalpine, February	38	10	17-65	4
Delano subalpine, May	824	567	192-3087	5
Fertilizer subalpine, May	220	71	42-385	4

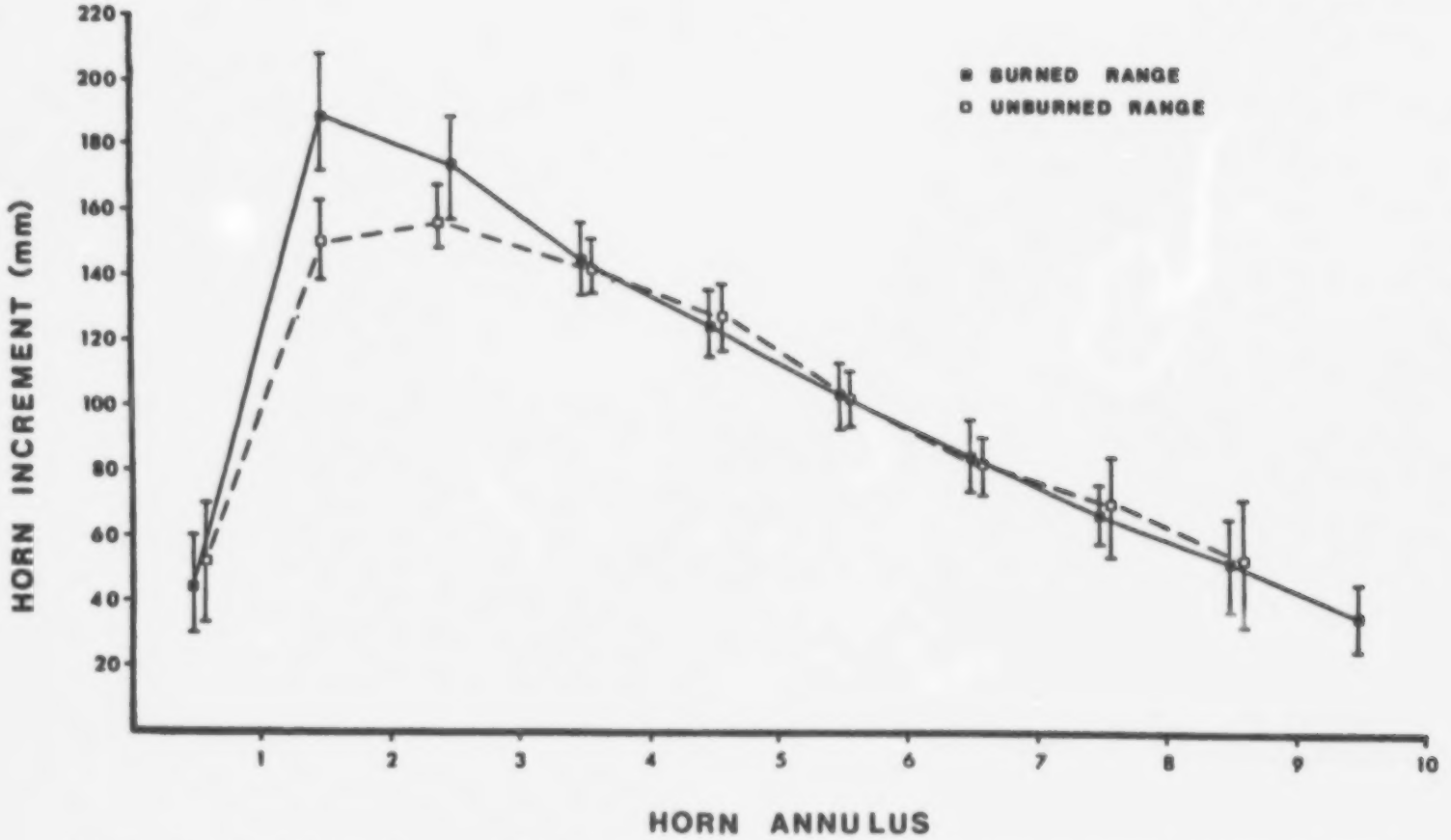

Figure 27. Comparison of annual horn increments of Stone's sheep rams on burned versus unburned range ($\bar{X}$ ± 95% C.I.) in northeastern British Columbia (1980-1982).

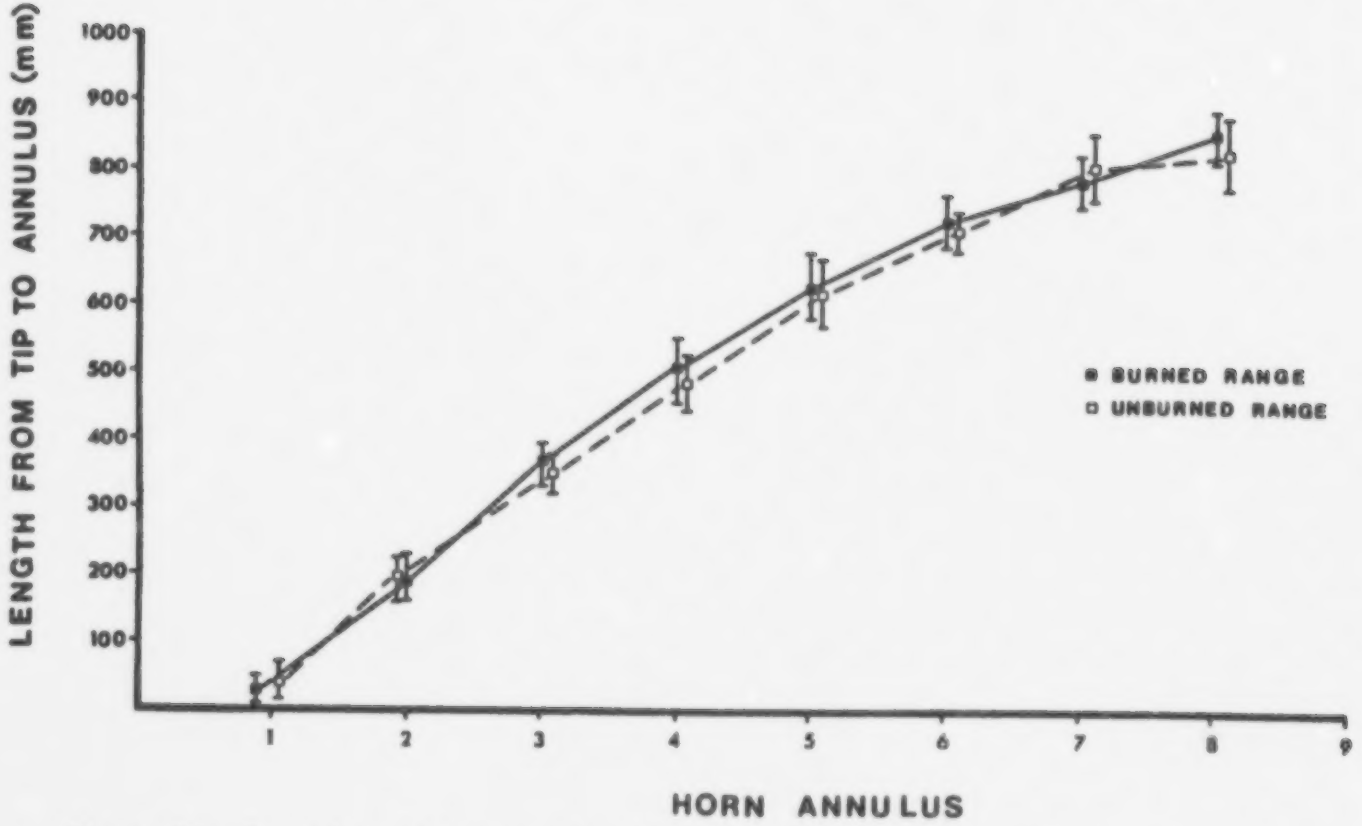

Figure 28. Comparison of horn lengths from tip to annulus of Stone's sheep rams shot on burned range and unburned range ($\bar{X}$ ± 95% C.I.) in northeastern British Columbia (1980-1982).

rams on unburned range (30.8 mm ± 7.9 (S.E.)). This difference was not statistically significant but it was sufficient to nullify the difference in horn growth between ranges. Although rams from burned range did not have longer horns, they may have scored higher as trophies because the thin tip was not included in the remaining horn.

POPULATION PARAMETERS

Population Numbers

The following population numbers are minimum counts. In addition, because most of the area was continuous sheep habitat, any boundary used to define a population would have been quite arbitrary.

The best counts are for the number of sheep wintering on the subalpine slopes of Fertilizer Mountain (Table 17). This group appeared to be discrete from other wintering groups and the numbers remained relatively constant throughout the winter. However, numbers were variable after the snow melted and animals could move around more easily.

Approximately 15-20 sheep used the alpine peaks of adjacent Toad Mountain in the winter, and spring counts usually found from 5-16 sheep on the subalpine slopes.

Winter aerial surveys of the Sulphur Creek area found 14-17 sheep on adjacent alpine peaks. In addition, another 22 animals were spotted on other mountains in the Toad River area that were not immediately adjacent to burned slopes. Overall, the Toad River/Sulphur Creek area supported at least 90 sheep in an area of about 900 km^2 for a minimum density estimate of 1 sheep/10 km^2.

Winter aerial surveys in the Yedhe/Delano area located from 40-50 animals on windswept alpine ridges. May counts in Delano valley ranged from 25-40 animals.

Summer counts (June-July) at the Churchill Mine site provided the best opportunity to obtain replicate counts over many days (Table 18). In 1982, eight collared sheep regularly used this mineral lick but on any one day only 2-5 of these individuals were spotted at the lick. Therefore, the total count on any day probably only included from 25-65% of the total number of animals using the lick. Thus, it was likely that a total of 100-125 sheep used this lick during the summer. The size of the area from which animals were drawn to this mineral lick

Table 17. Maximum daily count of sheep on Fertilizer Mountain each month (1980-1982).

Date	Ewes	Yearlings	Rams	Total
May 1980	8	7	12	27
March 1981	11	6	9	26
April 1981	11	8	5	24
May 1981	16	8	16	40
February 1982	16	8	9	33
April 1982	16	8	9	33
May 1982	14	7	6	27

Table 18. Number of sheep using Churchill Mine lick and adjacent areas in summer (1980-1982).

Date	Number
June 1980	52
July 1980	49
June 1981	36-49
July 1981	39-102
June 1982	24-76

was not known. The total area of adjacent watersheds from which these sheep appeared to be coming totaled about 800 km^2. This provided a rough estimate of 1 sheep/7-8 km^2.

Lamb And Yearling Counts

It was difficult to obtain accurate lamb counts in the Toad River area because by the time the lambs were born the sheep were in small groups dispersed widely in the Spruce-Willow-Birch zone. Counts of 9-month-old lambs (short yearlings) on Fertilizer Mountain were probably more reliable due to the discreteness of the population and the opportunity to obtain replicate counts. It was also difficult to obtain lamb counts immediately after lambing in the Delano/Yedhe area, primarily due to access problems. The most reliable counts were taken later in the summer at the Churchill Mine site where large, replicate samples were obtained.

In 1980, the lamb/ewe ratio was high in both the Fertilizer Mountain and Churchill populations following an early spring with subalpine slopes being snow-free by early March (Table 19). In 1981, the lamb/ewe ratio was almost four times greater near Toad River than at Churchill following an essentially snow-free winter on the burned, subalpine slopes but a high snow winter in the alpine. The 1982 lamb/ewe ratio was low in both populations following a severe winter with deep snowfall greatly restricting the available range in both areas. Thus high lamb production appeared to be related inversely to winter snow accumulation.

Survival Rates

The only direct data which gave any indication of survival rates were:

1) A minimum of eight adult ewes out of 10 collared in the summer of 1981 survived the winter and were seen in the summer of 1982.

2) All of the 33 animals using Fertilizer Mountain in January, 1982 survived until April, 1982.

These two points indicate that, in general, natural adult mortality rates were quite low.

Crude estimates of lamb winter mortality were made by comparing lamb/ewe ratios with the yearling/ewe ratios for the following year (Table 19). On Fertilizer Mountain, estimated lamb mortality was 12% during the mild winter of 1981 and 32% during the severe winter of 1982.

Table 19. Lamb/ewe and yearling/ewe counts of Stone's sheep on Fertilizer Mountain and at the Churchill Mine (1980-1982).

Location and Date	Lambs/ ewe	Lambs counted	Yearlings/ ewe	Yearlings counted
Fertilizer Mountain:				
June 1980	0.60	64	-	-
March 1981	-	-	0.53	17
June 1981	0.74	17	-	-
March 1982	-	-	0.50	8
November 1982	0.35	6	-	-
March 1983	-	-	0.38	20
Churchill Mine:				
July 1980	0.49	64	0.28	23
July 1981	0.18	22	0.27	32
June 1982	0.26	90	0.19	66

In the Churchill area, the estimated lamb mortality for 1981, a severe winter in the alpine, was 45%. The estimate for the winter of 1982 was unreasonable (i.e., more yearlings than lambs) due to a questionably low lamb/ewe ratio for 1981. The average for the three reasonable estimates of winter lamb mortality was 30%.

Group Size

The average group size was 4.8 ± 3.0 (S.D.) (n = 71). Most groups ranged from 3-6 in size but it was not unusual to see single sheep or pairs. Large groups of sheep (50+) often concentrated around mineral licks in summer. In winter, large groups (20+) sometimes occurred in areas where many sheep were restricted to a small area by snow.

DISCUSSION

SEASONAL PATTERN OF NUTRITION

A Model of Food and Energy Intake for Mountain Sheep

Within the model, I assume that a sheep will consume enough food to meet its energy requirements unless intake is limited to some lower level by passage rate through the gut. This general pattern is observed in domestic sheep (Dinius and Baumgardt 1970), cows (Conrad et al. 1964), and deer (Ammann et al. 1973).

Mountain sheep have a daily maintenance metabolic requirement of about 110 kcal/$W^{0.75}$ (Chappel and Hudson 1978) which is almost identical to the value for domestic sheep (NRC 1975). This value corresponds to a daily digestible energy requirement of 128 kcal/$W^{0.75}$. Hebert (1973) reported daily digestible energy requirements ranging from 112 - 156 kcal/$W^{0.75}$ for bighorn sheep. Actual energy requirements of an individual will often exceed the maintenance requirement depending on the physiological state (Table 20). The energy cost of grazing in domestic sheep is about 1.25 times the maintenance requirements of penned sheep (Osuji 1974). However, the energy requirements of mountain sheep in maintenance trials tend to be closer to values for grazing domestic sheep than to penned domestic sheep, possibly due to the stress associated with captivity of mountain sheep compared to docile domestic sheep. Therefore, an energy expenditure for grazing is not added to the maintenance level.

Table 20. Digestible energy requirements of sheep under different physiological conditions.

Physiological State	Digestible Energy Requirements kcal/$W^{.75}$	Multiple of Maintenance	Minimum Adequate DMD[a] %
Maintenance	128[b]	1.0	48.0
Early gestation	140[b]	1.1	49.0
Late gestation	232[b]	1.8	60.0
Lactation	319[b]	2.5	69.0
Lamb growth	339[b]	2.7	79.0
Adult weight gain of 0.02 kg/day	140[c]	1.1	49.0
Adult weight loss of 0.02 kg/day	115[c]	0.9	47.0
Maintenance + Thermoregulation below -20°C	178[d]	1.4	54.0

[a] calculated from the model

[b] NRC 1975

[c] Garrett et al. 1959

[d] Chappel and Hudson 1978

Gross energy content of most mountain sheep forages is about 4.3 - 4.4 kcal/g (Hebert 1973). The digestible energy content of forage can be estimated by multiplying the gross energy value by the dry matter digestibility (DMD) of the forage. Therefore, the food requirement of a mountain sheep can be calculated by the equation:

$$\text{Food requirement (g/day)} = \frac{(a)\ (128)\ (W^{0.75})}{(4.4)\ (DMD)}$$

where: a = multiple of maintenance requirement from Table 20,
W = body weight in kg
DMD = dry matter digestibility expressed as a proportion.

The maximum level of forage intake in ruminants is limited by the passage rate through the gut (Blaxter et al. 1961; Conrad et al. 1964). Because outflow from the animal is relatively constant (Phillipson and Ash 1965), the only way that food intake can increase is if more of it is digested. Therefore, intake increases as forage digestibility increases until energy requirements are met.

Data on intake rate versus forage digestibility when gut capacity is limiting are presented for domestic sheep and bighorn sheep in Fig. 29. The linear regression was calculated excluding the four low outlying points for which intake appeared to be well below the gut capacity. This relationship is used in the model to calculate maximum intake capacity.

The maximum possible energy intake will be the product of the maximum capacity and the digestible energy content of the food. Since DMD influences both of these values, changes in DMD have a multiplicative effect on energy intake when the digestive system is at capacity (Fig. 30). Therefore, small changes in DMD can have quite major effects on the energy intake of the animal.

In the model, I assume that the actual food intake of the animal will be whichever value, food requirement or maximum capacity, is least. That is, the sheep will feed to meet its energy requirements unless restricted to a lower consumption by gut capacity. The value for food requirements will depend on body weight, physiological state of the animal, and the DMD of the food. Maximum capacity is a function of body weight and the DMD of the food.

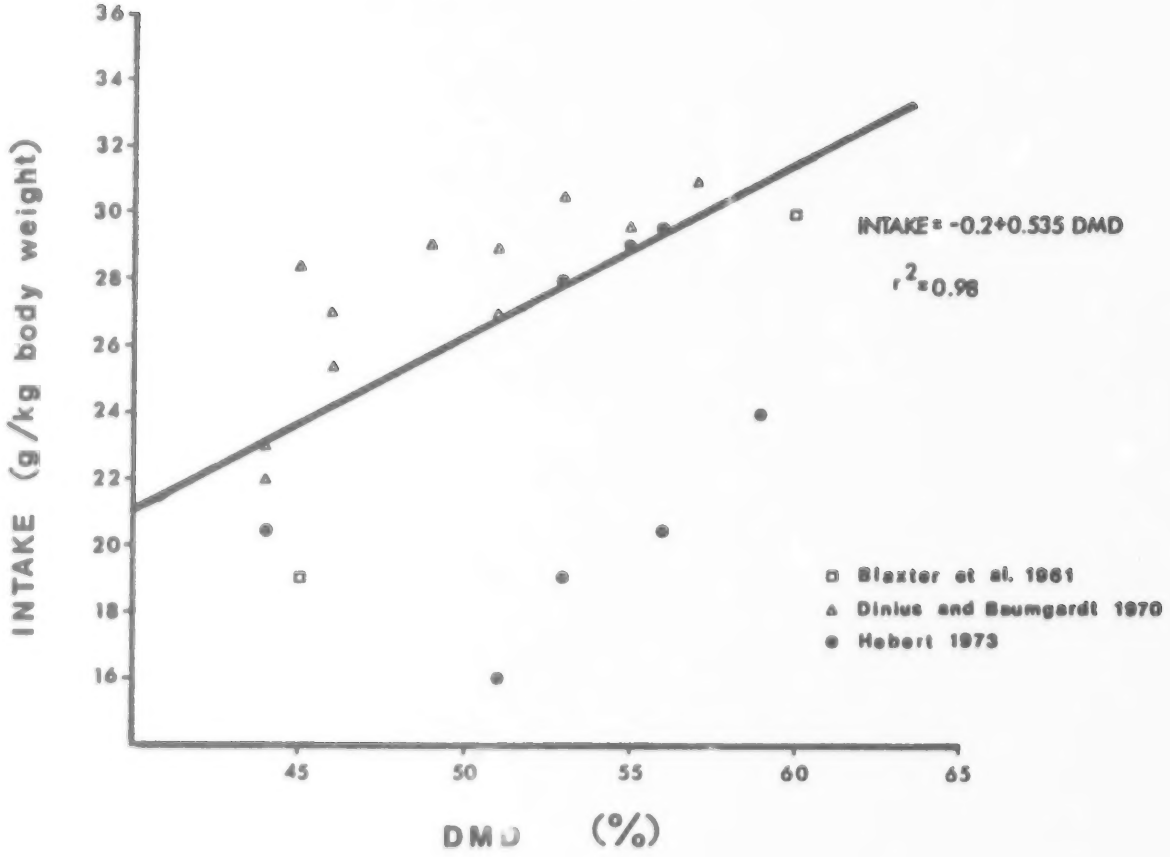

Figure 29. Relationship between digestibility of the food and the daily intake of sheep when digestive capacity is limiting.

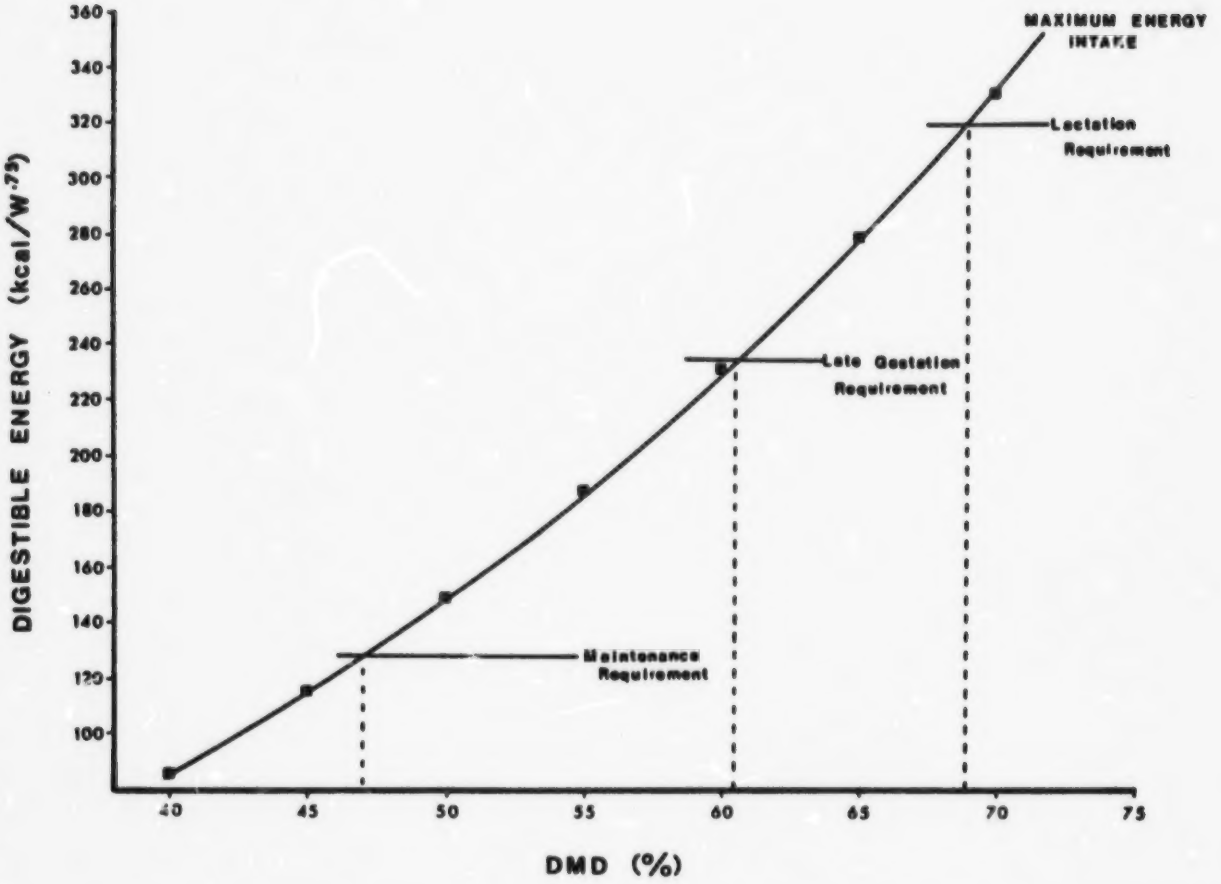

Figure 30. Relationship between digestibility of the food and the model's prediction of maximum possible daily energy intake of sheep.

Implications Of The Model

The value for DMD at which the calculated maximum energy intake (capacity limit) equals the energy requirements represents the minimum forage DMD that will provide the animal's energy needs (Fig. 30). Capacity is a function of body weight and forage DMD. The minimum forage digestibility on which a 50 kg sheep can meet its maintenance requirements is estimated to be 48%. At lower forage digestibilities, gut capacity will limit intake below the food requirement level. As energetic requirements increase, the minimum quality of forage required to meet demands will also increase (Fig. 30).

The annual pattern of energy requirements for a 50 kg adult ewe is presented in Fig. 31 based on the data in Table 19. Winter requirements were calculated assuming that about 25% of the days are below -20°C and require energy for thermoregulation.

The maximum possible energy intake will depend on the digestibility of the forage being consumed by the animal. Although forage quality measurements were collected throughout the season, fecal protein values (corrected for ash) were used as a measure of food quality from May to November because they indicate what the animal consumed rather than what was available. The DMD of the food was calculated from May to November from the fecal protein data using the regression equation presented by Lambourne and Reardon (1963). However, fecal protein values did not seem to predict reasonable values for food quality when quality was very low. In the winter, even when the sheep ate all the forage, fecal protein did not decline below an average of 10% even though forage protein was only 4% (Fig. 24). This disparity probably results from a decreased digestibility of protein at very low crude protein levels (Mould and Robbins 1981). Therefore, fecal protein does not distinguish between poor and very poor forages. This problem explains why fecal protein values failed to differentiate sheep condition between mild and severe winters and between alpine and subalpine winter range.

Because sheep consumed virtually all the forage available during a severe winter, the digestibility of the available forage represents the digestibility of the food eaten. This value was used as the forage digestibility for the winter months.

Given the DMD of the food, the maximum possible energy intake was calculated using the values for maximum capacity (Fig. 29) and digestible energy content of food

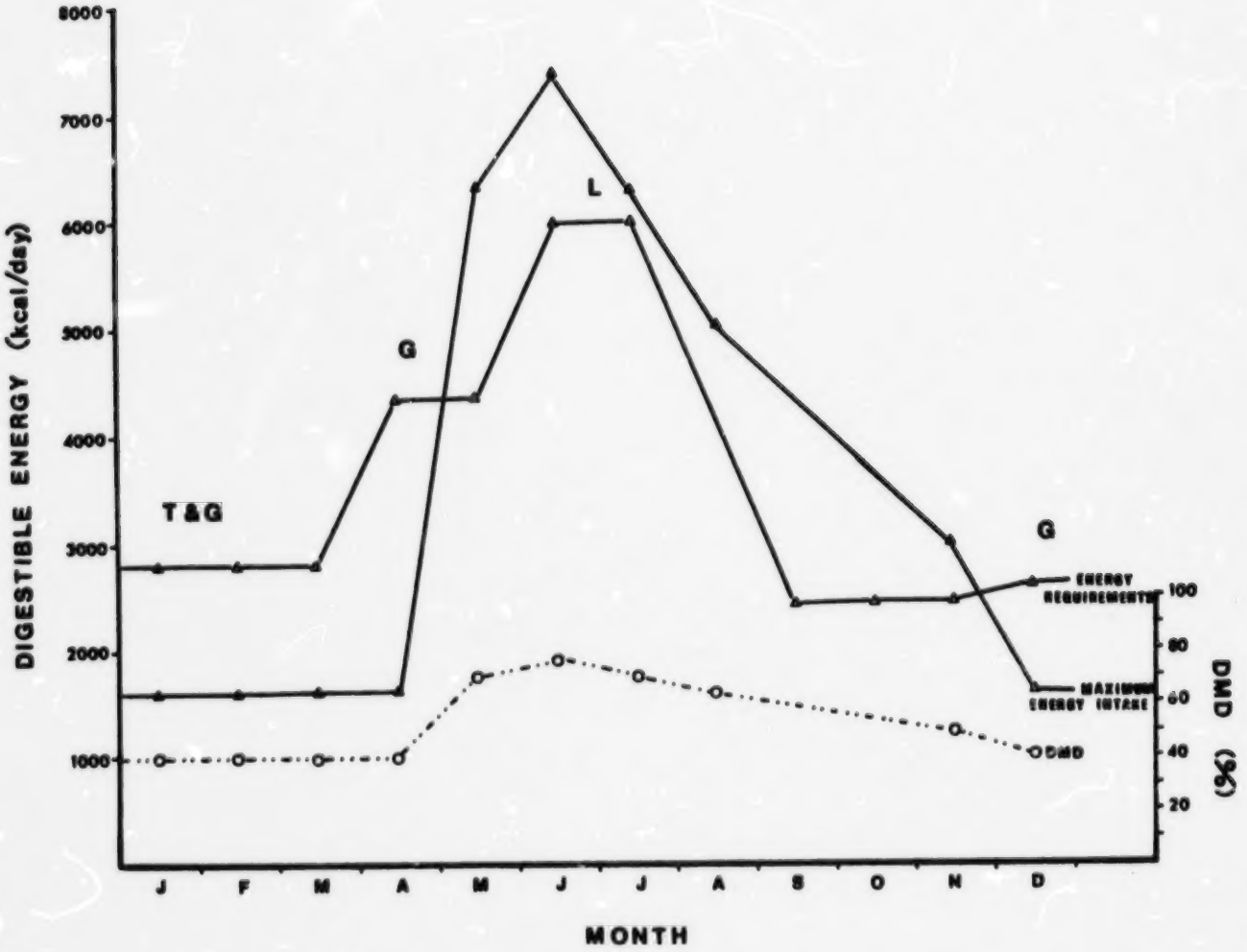

Figure 31. Seasonal pattern of daily energy intake and energy requirements of a 50 kg ewe predicted by the model.

(i.e. kcal/g = 4.4 x DMD). Requirements exceeded the supply in winter but were less than the supply in summer and early fall (Fig. 31). Over the season, the calculated energy deficit in winter (200,000 kcal) was balanced by the summer-fall surplus (215,000 kcal). The daily winter deficit of 1200 kcal/day would result in a daily weight loss of about 106 g/day (Garrett et al. 1959), for a total of about 12-13 kg over the winter. This value is comparable to the 18-22% overwinter weight loss reported for bighorn sheep during severe winters (Stelfox 1976). The energy surplus in summer and fall would allow the animals to put on fat for the next winter.

Captive mountain sheep and deer with access to high quality food ad libitum exhibit a voluntary reduction in food intake during the winter resulting in weight stasis in sheep and weight declines in deer (Chappel and Hudson 1978; Nordan et al. 1968). This phenomenon suggests that the metabolic pattern of wild ungulates is genetically programmed to correspond to the energy available in the wild. It is unlikely that wild ungulates voluntarily reduce their intake in the wild as suggested by Mautz (1978) but rather that they eat as much as they can given the limitations imposed by their digestive capacity. Voluntary reduction in captive animals is possibly an anomaly resulting from available food quality greatly exceeding demands which are programmed to correspond to natural food quality.

It may seem unusual that an animal does not have the capability of using abnormally abundant food energy when it is available. However, non-growing ungulates in winter have a maintenance metabolic rate below the level of animals which are physiologically geared to grow (Silver et al. 1969; Holter et al. 1977). This decrease is related to winter decreases in thyroxine and growth hormone levels (Bahnak et al. 1981). Therefore, maintaining the physiological ability to utilize surplus energy for growth in winter would entail a greater energy deficit under the usual winter conditions of a negative energy balance.

Elk and moose do not exhibit a weight loss in winter when provided with high quality food in captivity (Hudson, pers. comm.) which suggests that they are not programmed to lose weight in winter, presumably because winter forage in the wild is adequate to meet their maintenance metabolic requirements. Larger ruminants can meet their requirements on lower quality forage because as body size increases, the capacity of the digestive tract increases at a greater rate than the metabolic rate. The model predicts a minimum forage digestibility of 42% to meet the

maintenance requirements of a 200 kg elk and 39% to meet the requirements of a 400 kg moose. It is likely that they can obtain food of this quality in winter.

Another aspect to this relationship between body size and forage quality requirements is the importance of lambs growing to an adequate size to survive the winter (Bunnell 1980). The model predicts that a 30 kg lamb can meet maintenance needs on 50% digestible forage compared to 52% digestibility for a 20 kg lamb (Fig. 32). When DMD is below the maintenance requirement, small lambs will lose weight more quickly than larger lambs. Similarly, large rams will be able to survive on less digestible forage than ewes.

Protein Nutrition

The seasonal crude protein requirements for sheep are compared to the crude protein content available in the forage and the protein content of food predicted from fecal protein values in Table 21. Protein supply in forage was less than requirements during winter and early spring but forage crude protein content exceeded requirements during the summer months when new production was available. The fecal protein values were probably a dependable measure of food protein in the summer but they overestimated food protein in winter for reasons discussed previously.

Summary Of Seasonal Nutrition Patterns

Stone's sheep in winter were forced to eat forage which was too low in digestibility to meet energy requirements and was deficient in protein and many essential mineral elements. The animals were forced to rely on stored reserves for winter survival. The onset of new production in the spring provided high quality forage which exceeded the immediate requirements of the animals throughout the summer and allowed them to accumulate reserves for the next winter. The seasonal nutritional regime was mirrored by fecal protein and DAPA values.

SELECTIVE FEEDING

Range Selection

In winter, when Stone's sheep faced the most severe nutritional problems, they also faced the most severe restrictions of available range. Sheep were restricted to ranges with snow accumulations of less than 25-30 cm. This restraint dominated any possible selection for areas

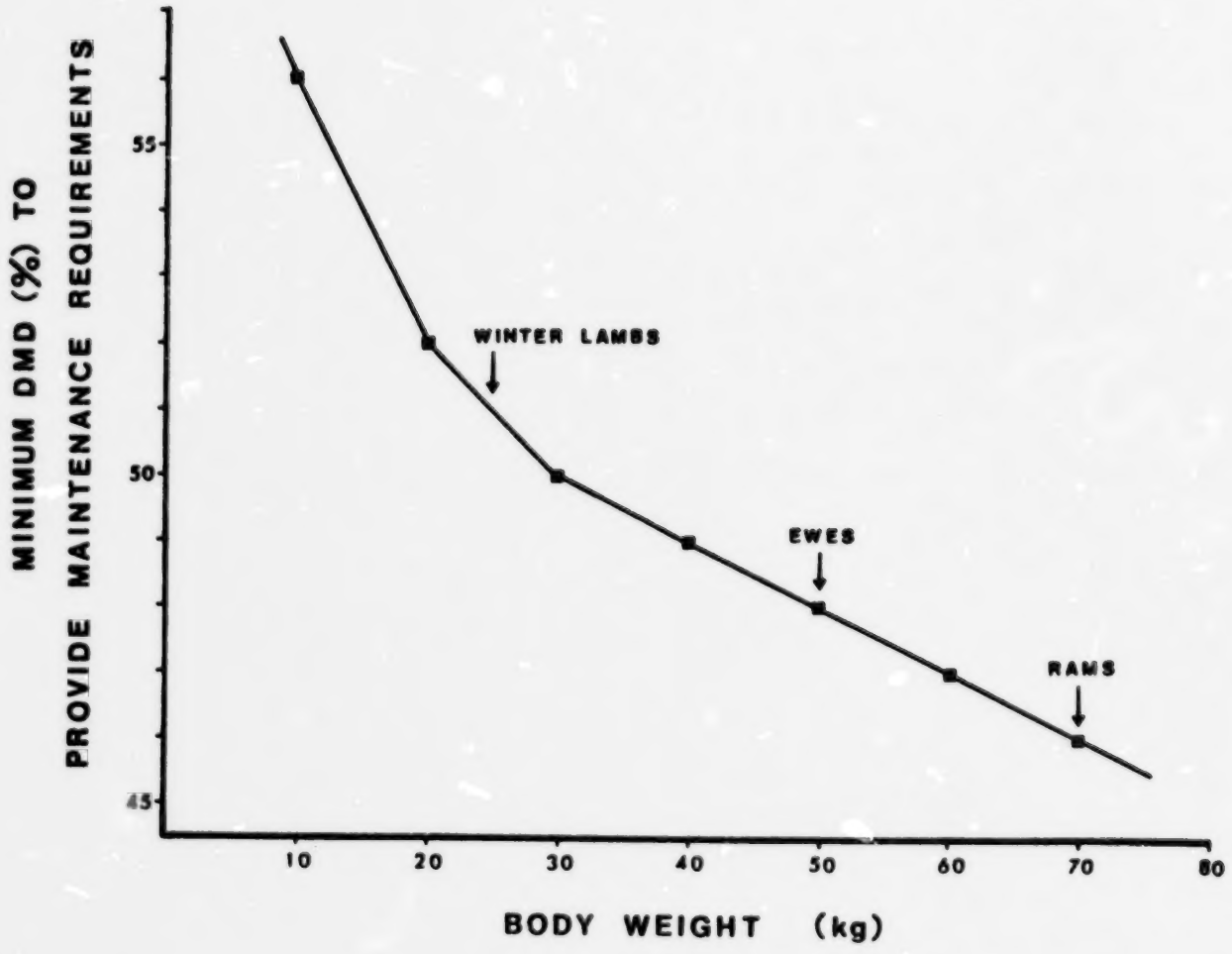

Figure 32. Relationship between body weight of sheep and the model's prediction of minimum forage digestibility adequate to meet maintenance requirements.

Table 21. Protein availability in forage on Stone's sheep ranges compared to protein requirements of domestic sheep.

	Requirements for Crude Protein in Diet[a]	Crude Protein in Available Forage	Protein Content of Food Intake[b]
	%	%	%
Winter:			
Early gestation	9.0	4.0	-
Ram maintenance	8.9	4.0	-
Spring:			
Late gestation	9.3	18.0	8.7 -20.0
Summer:			
Lactation	10.4	18.0 - 25.0	21.0
Lamb growth	16.0	18.0 - 25.0	21.0

[a] NRC 1975.

[b] estimated from fecal protein using the equation from Hebert (1973):
% Crude Protein in Diet = -0.94 + 1.034 x % Fecal Protein.

with more or better food. Sheep used both alpine and subalpine ranges in winter so long as they were not covered in deep snow. The role of snow in restricting range use of sheep is also reported by Geist (1971), Hoefs and Cowan (1979), and Simmons et al. (1981). Selection of ranges in winter was thus selection for available food rather than for areas with abundant but snow-covered forage.

Avoidance of areas with high snow depths would act to reduce energy expenditures for locomotion. Mountain sheep are poorly adapted for movement through snow with their low chest height and high foot-loading (Telfer and Kelsall 1971). Also, if their food is covered by deep snow they must spend a large amount of time digging to reach it (Fig. 25). The influence of snow depth was the major factor which limited the value of range burning for Stone's sheep. Abundant forage on the burned slopes was usually unavailable to the animals at the critical time of the year.

Movement to subalpine areas in spring provided the sheep with nutritious new production far earlier than it was available on alpine ranges (Figs. 8 and 9). The gradual movement to higher elevations throughout June and early July continued to provide sheep with the best forage available. In summer, the alpine range used by sheep provided more nutritious forage than was available on the subalpine slopes. In fall, when forage quality was declining on all ranges, sheep were the least selective and used a great variety of range types. The nutritional benefits of the altitudinal migration of mountain sheep were studied in detail by Hebert (1973). During the altitudinal migration the sheep are usually moving from areas of abundant low quality food to areas of sparse but high quality food.

Use of mineral licks in summer had important effects on the range use patterns of the sheep in this and other studies (Simmons 1982). Sheep are usually found close to mineral licks in summer. Although some sheep used subalpine licks in summer, they returned to the alpine range for foraging. Sheep appeared to use licks to obtain sodium as in other studies of ungulate mineral licking (Fraser et al. 1980). Most forages do not contain adequate amounts of sodium to meet body needs (Maynard et al. 1979) and licking behaviour appeared to satisfy this need. Requirements for other essential elements could be supplied by summer forage which were higher in these elements than the mineral licks.

Overall, the seasonal pattern of movements by Stone's sheep resulted in the animals feeding in areas with the most nutritious available food while also satisfying their sodium demands in summer.

Selection Of Forage Species

Stone's sheep avoided eating several plant species which constituted a large amount of the total available forage biomass. Plants which were avoided apparently were not less nutritious than other foods (see Betula spp. and Arctostaphylos spp., Table 5) but rather had characteristics which made them unpalatable. These mechanisms were not quantified but included waxy and/or leathery cuticles on Arctostaphylos spp., Dryas spp., and conifers, and sticky secretions on Betula glandulosa.

Forbs were usually more nutritious than graminoids (lower fibre, higher protein) on spring and summer ranges. However, sheep did not appear to select forbs preferentially over grasses in spring and selected against forbs in summer. This is contrary to the optimal foraging hypothesis but may be due to higher levels of secondary compounds in forbs compared to graminoids which make them less palatable. There were numerous forbs on the ranges which are known to be toxic including Lupinus spp., Aconitum spp., Delphinium spp., and Zigadenus spp. (Stephens 1980). Most of these plants can be consumed in small quantities but are toxic when a large amount is eaten. Levels of toxic compounds tend to be lower in new plants than in mature ones (Freeland and Janzen 1974). Therefore, the selection against forbs in summer may have been due to high levels of toxic compounds in many species of forbs.

Selection Of Superior Quality Forage

Comparison of food quality (estimated from fecal protein values) with the quality of forage which was collected at random suggested that the sheep were not selecting better than average quality food, at least in terms of protein. The lack of a difference suggests that forage on a range may be quite homogeneous in quality and there was no need to be highly selective. Alternatively, sheep may have been unable to distinguish between differences in quality at that level.

Selecting A Mixed Diet

According to the food quality data, Stone's sheep could have fed on only willow shrubs in the summer and obtained a very nutritious diet. The same could be said

for other food types at this and other times of the year. Although sheep did feed heavily on particular food types at certain times of the year, they always maintained a varied diet. Westoby (1978: 627-628) discussed the biological bases of varied diets:

i) A reduction of search costs will result from taking several foods of equal value.

ii) If the optimal food type changes with time, the diet will contain a mixture of these foods.

iii) Animals may have to sample a variety of foods to determine the optimal food.

iv) If different foods are the best source of different nutrients (or non-sources of negative compounds) the optimum diet will be mixed.

All of these reasons may apply to Stone's sheep.

Sexual Differences In Selectivity

Differences in body size and energetic demands might be expected to cause differences in forage selectivity between rams and ewes. The model predicts that a 70 kg ram can meet maintenance requirements on 46% digestible forage compared to 48% for 50 kg ewes. Geist and Petocz (1977) suggested that differential range use between sexes in bighorn sheep may be related to differences in foraging strategy. However, Shank (1982) studied the same population and concluded that it was unlikely that this spatial separation arose from differential diet preferences. In the present study, spatial separation of sexes onto distinct ranges did not occur. Over short periods of time, ram groups were often spatially separate from ewe groups but in all seasons they regularly made use of the same areas of the range. Therefore, spatial separation of rams and ewes was not due to differential range preferences.

Alternatively, one might predict that rams would eat lower quality food than ewes because they can meet their requirements with less digestible forage. Shank (1979) found no difference between food quality of rams and ewes in winter. The lack of a difference might have been expected because both sexes were below maintenance in winter and should have selected the best food available. However, in summer, rams might be expected to select poorer forage if it was very abundant allowing them to meet their requirements in less time than by being highly selective. In fact, there was no difference in the food

habits or the food quality as measured by fecal protein and DAPA levels between rams and ewes in summer. Therefore, there was no reason to believe that sexual differences in food selectivity exist in Stone's sheep. The lack of a difference is further evidence that sheep do not have to be highly selective when feeding in summer. There was no lack of high quality food once the animals had selected the best range.

Summary Of Food Selectivity

Stone's sheep selected the range which contained the most nutritious available forage. Certain foods were avoided, probably because of plant characteristics which made them unpalatable. Beyond these initial levels of selectivity, sheep did not seem to select forage which was any more nutritious than the average food available. Apparently once the sheep had selected the best range and avoided unpalatable foods, there was no need or opportunity to feed more selectively.

INTAKE RATE

Both biting rate and foraging time were independent of available forage biomass. This point was particularly evident in the lack of any difference in the spring between sheep on burned range compared to natural clearings. Although the grass length was similar on both areas, burned ranges had a much higher forage biomass due to a greater density of grass tillers. The results were consistent with data for domestic sheep in which biting rate and intake rate are primarily dependent on the tiller length rather than the tiller density (Allden and Whittaker 1970; Arnold 1975). Bite size of domestic sheep declines at short tiller lengths (Allden and Whittaker 1970). Smaller bite size is partially compensated for by an increased biting rate and by longer foraging periods but this compensation is incomplete when grass tiller length is very short resulting in a decreased daily intake. This pattern is similar to that reported for grazing cows (Chacon and Stobbs 1976), but differs from reindeer in which bite size remains quite constant and intake rate is determined by the biting rate which increases as forage biomass increases (Trudell and White 1981). It was not possible to investigate the relationship between tiller length and biting rate of Stone's sheep because the altitudinal migration of the sheep resulted in them always feeding in areas where the tiller length was about 8 - 12 cm (Fig. 8).

When the sheep were on spring range, the model predicted a maximum daily food capacity of a ewe feeding on 65% digestible forage to be about 1837 grams. Dividing this value by the number of bites/day (23000) gives an estimated bite size of 0.08 grams. This value is almost identical to the value for domestic sheep feeding on 8 - 10 cm long grass (Allden and Whittaker 1970). It is also close to the weight of an individual grass plant of that length (Fig. 10) suggesting that most bites consist of an individual small grass tiller. The estimated intake rate is about 2.7 g/minute if they were consuming their maximum capacity of food. It is interesting to note that domestic sheep can attain their maximum rate of intake on 8 - 10 cm grass with a bite size of 0.08 g (Allden and Whittaker 1970; Arnold 1975). These observations suggest that by following the zone of 10 cm grass, Stone's sheep were able to maximize intake rate while simultaneously feeding on the highest quality of grass available (Fig. 19). Such behaviour is consistent with the optimal foraging hypothesis, i.e. maximization of net energy intake rate (Schoener 1971). However, the calculated intake rate of the sheep was only about half the maximum reported for domestic sheep (Allden and Whittaker 1970). The difference resulted from Stone's sheep biting at only about half the rate (33 compared to 60 bites/minute). By feeding for almost twice as long (700 vs 400 minutes) Stone's sheep took about the same number of bites/day as the domestic sheep studied by Allden and Whittaker (1970). This difference between domestic sheep and Stone's sheep may indicate that Stone's sheep on natural range were unable to attain the same biting rate as domestic sheep on planted pasture. Alternatively it may result from sheep reducing their biting rate to a more relaxed level when they are not pressed to feed quickly. The latter hypothesis is supported by the fact that domestic sheep do not usually forage at the maximum possible rate but rather vary the rate depending on their needs. Arnold and Birrell (1977) found that fat sheep and thin sheep on good pasture both foraged for the same length of time but that the thin sheep had a higher intake over that time (2.2 vs 1.8 g/minute). Similarly Arnold (1975) found that lactating sheep foraged slightly longer than dry sheep but that the most important factor allowing them to increase their daily intake was a greater intake rate (2.17 vs 1.82 g/minute). Therefore, sheep do not usually feed at the maximum rate possible but slow down to a more relaxed rate if they can. Thus sheep are not "time minimizers" when foraging. Actually there is no reason to expect sheep to eat at a frantic rate only to provide more time for resting. The energy expenditure required for this rapid foraging may well be as great or greater than energy saved by resting. Thus a conservative rate of foraging may

actually be a strategy of "energy maximization".

The rather constant biting rate of Stone's sheep under different conditions suggests that this was the "comfortable" rate for them to maintain. Foraging time then becomes a function of the daily food intake of the animals which in turn is determined by requirements or capacity. Because the seasonal intake of the sheep is roughly correlated with the amount of daylight (i.e., low intake in winter, high in summer), a constant intake rate would result in the animals feeding for about the same proportion of the daylight hours (Table 22).

Foraging activity which covers 60-70% of the daylight hours is quite standard for domestic sheep under good range conditions but sheep which are unable to meet their needs will forage for a much greater proportion of daylight (Arnold 1960b; Allden and Whittaker 1970).

Overall, there appears to be a great deal of similarity between the foraging behavior of Stone's sheep and domestic sheep. The most important point is that Stone's sheep can maintain an adequate intake rate on ranges which are very low in plant biomass because intake rate is influenced primarily by grass length. A range which is poor for sheep is one on which grazing has resulted in very short grass (< 5 cm). Mountain sheep ranges may have very sparse grass cover but the grass is usually long enough to allow a high intake rate. For this reason, natural subalpine clearings appeared to allow the same intake rate as burned ranges in spring.

The consistently lower proportion of daylight time spent feeding by rams compared to ewes could be due to a greater intake rate or a lower food requirement. In the winter when the large rams have a greater food requirement, the difference is probably due to a greater intake rate resulting from a larger mouth size. Allden and Whittaker (1970) found that larger sheep had a greater intake rate when food was abundant. However, in the spring when the intake rate would be largely limited by the small size of new green plants, a large mouth would not likely provide an advantage. Therefore, the spring difference may reflect a difference in the food requirements of rams compared to ewes (1106 g/day for ram growth vs 1406 g/day for late gestation). The difference in foraging time between ewes and rams may explain why they forage in separate groups. Even without any active avoidance between sexes, differences in foraging time will lead to separate foraging groups. Ram and ewe groups often foraged or rested together. However, the ewes soon became spatially separated because they would move away

Table 22. Estimated foraging time of a Stone's sheep ewe in different seasons assuming a constant intake rate.

	February	May
DMD	40%	70%
Estimated intake (g)[a]	900	2025
Foraging time (minutes)[b]	360	810
Daylength (minutes)	600	1320
Proportion of Daylength foraging	60%	60%

[a] calculated from model

[b] assuming intake rate of 2.5 g/minute.

while foraging, leaving the resting rams behind.

A large biomass of dead forage appeared to have a negative effect on foraging on spring ranges. Sheep on burned spring range avoided areas with large amounts of dead grass, presumably because it interfered with their access to nutritious new production. This phenomenon is similar to the situation in which small African antelope forage on highly nutritious small plants which are exposed after larger antelope remove the bulk of the forage biomass (Vesey-Fitzgerald 1960). Moderate grazing by cattle is also thought to improve range for mule deer by exposing new growth (Wilms et al. 1979).

Food supply was not a problem for Stone's sheep in spring and summer when forage production on all ranges exceeded the requirements of the sheep (Table 23). However, winter ranges did not contain enough food in winters of high snowfall to meet the requirements or even the capacity limitations of sheep (Table 23). By late winter, sheep had essentially no food to eat.

For most of the year, the sheep had no problem getting enough food but endeavoured to obtain high quality food. The altitudinal movements from a high-biomass of low quality food to areas of sparse, high quality food served this objective.

ANIMAL CONDITION AND GROWTH

Poor winter nutrition of mountain sheep is correlated with high lungworm levels which can lead to major die-offs (Stelfox 1976). The poor winter nutrition of Stone's sheep, particularly of alpine sheep, was reflected in fairly high lungworm levels. Restriction by snow of sheep to small areas during the winter may also have led to increased transmission of the parasites. However, these levels were not as high as those leading to die-offs (> 1,400 larvae/g) in bighorns. Also, sheep were never observed to be coughing as in heavily affected populations (W. Samuel, pers. comm.). Death due to lungworm was probably not a major cause of mortality in these Stone's sheep populations but the difference in lungworm levels between alpine and burned subalpine winter range suggests superior nutrition on subalpine burns. In fact, lungworm levels may be a better indicator of animal condition than the fecal protein or DAPA levels during winter. Burning may also reduce lungworm levels by killing snails on the range which are the alternative host to the parasite.

Table 23. Forage availability of several Stone's sheep ranges compared to estimated sheep requirements.

a. Winter Range

Location	Available Forage kg	Number of Sheep	Forage Requirements[a] kg/100 days
Alpine (ridge above Churchill mill)	1500	15	1900
Subalpine (Fertilizer Mountain)			
high snow winter (1982)	4000	35	4500
low snow winter (1981)	80000	30	3800

b. Spring Range

Location	Graminoid Production kg/day	Number of Sheep	Forage Requirements[a] kg/day
Subalpine Burned (Fertilizer Mt.)	900	25	45
Natural subalpine clearing (slope shown in Fig. 5)	90	10	18

[a] Requirements calculated from the model assuming intake limited by capacity.

Data on body weights and measurements were inadequate to examine seasonal and inter-population differences. A summary of these data is presented in Appendix B.

Horn growth data showed that yearling rams had superior horn growth on burned range. Horn growth of rams is primarily dependent on spring nutrition (Bunnell 1978). Because other indicators of spring range quality showed no major difference between burned and unburned range, the poorer horn growth of yearling rams may have been due to the sheep from alpine winter range coming onto the spring range in much poorer condition. Yearlings from the alpine winter range appeared to be smaller than yearlings from subalpine winter range. The horn growth of older rams did not differ between ranges and the initial disparity due to better yearling growth had been lost by the time the animals were shot by hunters. Although the horns from burned range were not longer, they may have been better trophies since they tended to have more tip broomed off. Therefore, range burning may have a slight beneficial effect on the production of trophy rams.

POPULATION DYNAMICS

Adult survival rates appeared to be quite high based on the small sample of collared animals (minimum survival of 80%) and the 100% survival of ewes throughout the winter of 1982 on Fertilizer Mountain. Low mortality rates for adult mountain sheep (< 15%) are common (Simmons et al. 1981; Hoefs and Cowan 1979; Geist 1971). Typically, annual losses to predation and other mortality causes are very low (< 10%) for prime aged sheep but mortality rates increase for old-aged adults (> 8 years old).

Low lamb:ewe counts were the most obvious factor likely to affect population growth. It is not surprising that lamb production is often quite low considering the poor nutrition of the pregnant ewes during winter. Poor nutrition during gestation results in the birth of undersized lambs which experience a high mortality rate even under ideal conditions following birth (McClymont and Lambourne 1958). A similar situation occurs in deer and elk (Thorne et al. 1976; Verme 1977). Heimer (1983) reported lower fetus weights associated with a reduced lamb:ewe ratio in Dall's sheep. The experimental data which are most comparable to mountain sheep are presented by McClymont and Lambourne (1958). Sheep were placed on poor nutrition during gestation until 4 weeks pre-partum and then given high quality feed. Ewes that had lost 22% of their body weight produced lambs which experienced a

26% peri-natal mortality whereas ewes which had lost 25% body weight lost 41% of their lambs at birth. Based on the model, these values for weight loss correspond to daily digestible intakes of 63.8 kcal/$W^{0.75}$ and 56.0 kcal/$W^{0.75}$ respectively. Under better nutritional conditions, Prior and Christenson (1976) found that ewes receiving 120 kcal/$W^{0.75}$ digestible energy throughout pregnancy suffered 10% peri-natal lamb mortality compared to only 2% lamb loss for ewes receiving 200 kcal/$W^{0.75}$ digestible energy. This relationship is shown in Fig. 33.

In the wild, an average lamb mortality of 18% would usually be added to these peri-natal losses before most reported lamb:ewe counts are made (Hoefs and Cowan 1979). Also, many studies, including this one, included 2-year-old ewes in the count. Yearling females do not breed in most sheep populations (Hoefs and Cowan 1979). I did not observe any 2-year-old ewes with lambs in the present study. Lamb/ewe counts which do not distinguish 2-year-old ewes will underestimate the lamb/adult ewe by about 15%. These data were used to generate a hypothetical relationship between winter nutrition of the ewes and subsequent lamb:ewe ratios in the summer (Fig. 33). These predicted values cover the normal range of reported lamb:ewe ratios (Hoefs and Cowan 1979). The lowest values (45-50 lambs/100 ewes) correspond to an estimated forage digestibility of about 35% whereas values of 60 lambs/100 ewes correspond to an estimated forage digestibility of about 40%. These digestibility values were the values for heavily grazed versus ungrazed areas of Stone's sheep winter range. Domestic sheep and cows similarly degrade the quality of their range over time by removing the best forage and leaving only poor forage remaining (Arnold 1960a; Chacon and Stobbs 1976). Heavy grazing which degrades the quality of the available forage in winter would be expected to result in lower lamb crops the subsequent summer due to poorer nutrition of the ewes. The impact of grazing on the range will vary depending on the population size, the initial amount of food available, and the degree of range limitation which is primarily a function of snow depths. Thus both density-dependent and density-independent factors will be operating. The negative effect of snow depth on lamb production was obvious in the present study and was also reported by Smith and Wishart (1978) and Nichols (1978). Hoefs and Brink (1978) found that lamb production appears to be related to forage quantity on the winter range. The negative impact of density on lamb production is reported by Woodgerd (1964) and Smith and Wishart (1978).

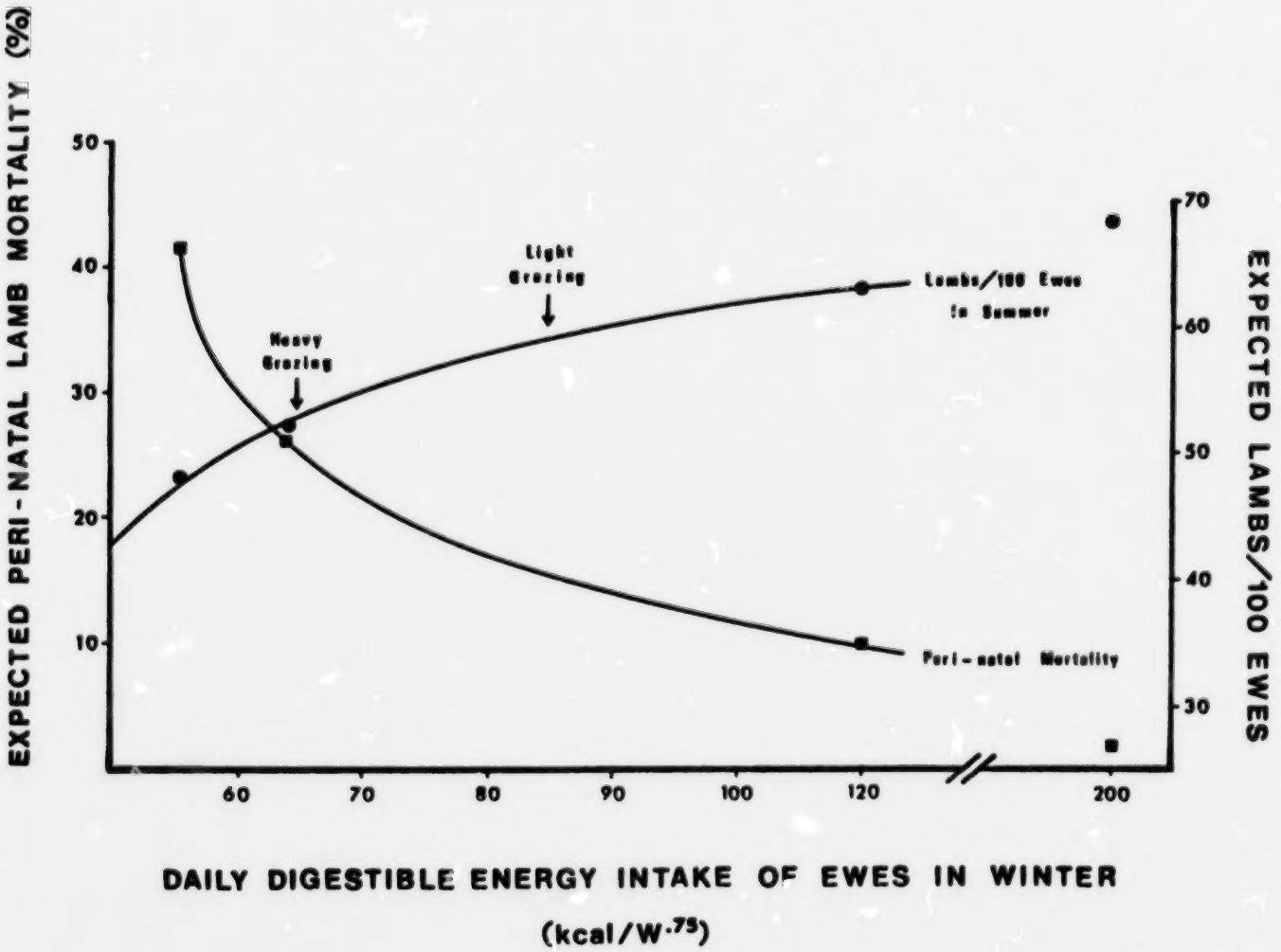

Figure 33. Relationship between daily energy intake of ewes in winter and the predicted values for peri-natal mortality and summer lamb/ewe ratio (2-year-old and older ewes).

The predicted lamb:ewe ratio following a mild winter (60-65/100) during which grazing intensity was low was comparable to the observed values for 1980 and 1981 on Toad Mountain. The predicted lamb:ewe ratio for severe winters, when grazing pressure was intense, was an overestimate compared to the results for Fertilizer Mountain in 1982 and Churchill in 1981 and 1982. This disparity may indicate that the relationship in Fig. 33 underestimates lamb mortality in poor conditions. Alternatively, the lower lamb production may indicate that maternal nutrition was even poorer than was predicted on the basis of forage digestibility. That situation could result from the animals being unable to obtain a sufficient quantity of food to meet even their capacity-limited intake needs. Considering the almost total removal of forage from winter ranges in 1982, this possibility seems to be quite likely. Overall, observed lamb crops in the study were consistent with predictions based on maternal nutrition during the previous winter.

The model predicts that no lamb should be able to survive the winter because a forage digestibility of 40% would result in a 30% weight loss. Poorer quality forage or lack of forage resulting from heavy selective grazing would make the situation even worse. Mule deer die when they lose about 28% of their body weight (deCalesta et al. 1977). However, a comparison of January weights of Dall's sheep lambs (27-39 kg; Bunnell and Olsen 1976) with June weights of Stone's sheep yearlings (19.1-30.4 kg) suggests that a 30% winter weight loss may be tolerable to lambs because Dall's sheep and Stone's sheep are almost identical in size (Appendix B). Certainly lambs did survive the winter although mortality rates were quite high (12-45%). Reported lamb winter mortality rates typically range from 30-50% (Hoefs and Cowan 1979; Simmons et al. 1981).

Although lamb mortality is probably at least partly density and nutritionally dependent, these relationships are not well quantified. However, if we apply an average winter mortality rate of 40% to the predicted lamb crop under heavy versus light grazing pressure (i.e., 50 vs 60 lambs/ewe) the result is 30 versus 36 yearlings/ewe respectively. A subsequent yearling mortality rate of 10% (Simmons et al. 1981) would leave 27 versus 32 two-year-olds or about 13 versus 16 female recruits/100 adult ewes. The higher number of recruits would result in slight population growth. The lesser number is insufficient to balance the adult mortality rate of 15% and would result in a population decline. The decline would be even more severe if an absolute lack of food in winter led to even lower lamb production. These rough calculations outline

the way in which density-dependent selective grazing could regulate population growth by way of ewe nutrition during pregnancy. However, this simple pattern will be masked by density-independent variability in winter severity and other regulatory factors.

MANAGEMENT OF STONE'S SHEEP

Stone's sheep heavily graze their limited winter ranges which results in severe nutritional problems and reduced lamb crop. Spring and summer ranges provide abundant, high quality forage and are not limiting. Therefore, any habitat improvement should be directed at improving winter range. Burning of subalpine range produces very productive grassland areas which are used by sheep. However, these areas are usually unavailable to sheep in winter because of deep snow. This problem severely limits the value of range burning for Stone's sheep. In the one exceptional area where subalpine, burned range was wind-blown and available to sheep in winter, the sheep appeared to benefit from the abundant food available. Therefore, future burning efforts should be directed towards areas which will be wind-blown in winter. The rarity of such areas compared to the large areas of range that have already been burned suggests that this may not be very feasible.

Although burned spring ranges contain much more forage than unburned ranges, sheep do not seem to benefit greatly from it. Because the intake rate of sheep is limited by bite size rather than the biting rate, ranges with very abundant food are not necessarily better than ranges with very sparse forage so long as the food is of high quality and the absolute quantity is not limiting. Therefore, burning to produce spring range does not appear to be justified.

Although range burning does not seem to be of any great value to Stone's sheep, it is not in any way detrimental and probably benefits other species such as elk. If range burning is continued in the area, it would be advisable to produce smaller burns rather than burning entire valleys. The small burn in Delano valley produced super-abundant forage far beyond the needs of the sheep and mountain goats which used it. Even if range burning was beneficial, there is no reason to expect that vast burned areas are superior to small burns. Forested areas provide habitat for furbearers, birds, etc., and may be used as thermal cover by ungulates and provide arboreal lichens for caribou. Therefore, a mixture of forest and small burns would probably support the greatest number and

diversity of wildlife.

Improvement of alpine winter range is probably not feasible. Fertilization in the alpine failed to increase the quantity or quality of forage (Appendix C), probably because plant production or nutrient cycling processes are limited by climatic factors. Also, the cost of any extensive fertilization program would likely be prohibitive. Overall, the value of habitat improvement programs appears to be extremely limited for Stone's sheep in this area.

Habitat destruction is not a major threat to most sheep populations with the exception of hydro-electric reservoirs which may flood critical subalpine, spring range. Stone's sheep acclimatize very well to disturbances such as roads and mines. Such developments are unlikely to cause any serious harm. The major problem is likely to be increased poaching related to improved access to new areas. This problem could be dealt with by strict law enforcement or preferably by controlling access to the areas.

Predator control has been proposed recently to increase Stone's sheep populations in the area. However, there is no good evidence that predators have a major effect on sheep populations. Wolf control in Alaska resulted in improved survival of moose and caribou calves but failed to increase the lamb survival of Dall's sheep (Gasaway et al. 1983). All predation attempts observed during this study were unsuccessful because the sheep were able to escape into precipitous terrain. Adult survival rates appeared to be high as in other studies of mountain sheep. Lamb production and lamb survival was related to winter severity. The sheep encounter severe nutritional problems related to high densities on restricted winter ranges. Therefore, any improvement in survival rates caused by predator control would only increase the negative impacts of high densities on winter ranges. It is unlikely that the winter ranges can support any more sheep.

Trophy hunting of large rams probably has no significant impact on the population numbers. There are more than enough mature rams to breed all the ewes. I am very skeptical of the hypothetical arguments against trophy hunting proposed by Geist (1970). This skepticism is supported by results of Shackleton (1973) and work in Montana (J. Ford, pers. comm.) which failed to find detrimental effects related to reduced numbers of large rams in the population.

Therefore, hunting regulations are primarily directed at ensuring that populations continue to produce large trophy rams. This objective is being effectively met by protecting small rams from hunting by full-curl or greater regulations. Also, outfitter quotas are based on the average age of sheep killed in the outfitting area the previous year. It would be more logical to base quotas on the size of sheep rather than the age since it is unreasonable to expect hunters to age free-ranging sheep accurately. Also, the size of sheep killed by resident hunters should not be involved in calculating outfitter quotas since resident hunters shoot significantly smaller and younger rams (Hurd and Masters, unpubl. data). Present demand by hunters is sufficiently great that most rams are probably killed within a year or two of reaching legal size. Therefore, to produce large trophy rams, smaller rams must be protected until they reach that size.

The major controversy in setting hunting regulations is dividing the kill between residents and guided non-residents. In terms of economic benefits to the area and the province, the value of a sheep taken by a guided non-resident is far greater than a sheep killed by residents. However, political pressure by resident hunters leads to progressively lower quotas for non-resident hunters. Such a debate is beyond the role of a biologist to decide.

CONCLUSIONS

The order of conclusions corresponds to the order of hypotheses presented in the Introduction

1) Forage quantity was much greater on burned ranges but forage quality was similar on burned and unburned ranges.

2) Quantity of food intake was similar on burned and unburned ranges for most of the year although quality began to increase a few days earlier on burned spring range.

3) Sheep selected ranges with the most nutritious available forage. Availability was severely restricted by snow in winter.

4) Quality of intake was not superior to the average quality of available herbage on the range. Structural and chemical factors affecting palatability appeared to be more important than quality in determining food selectivity.

5) Altitudinal migration to areas where tiller length was about 10 cm provided the opportunity for the sheep to maintain the maximum intake rate of high quality forage. However, sheep did not appear to feed at the maximum possible intake rate.

6) Foraging time and biting rate did not vary with changes in forage quantity.

7) Foraging time and biting rate did not differ between burned and unburned range.

8) Heavy grazing on winter range removed all the available forage during a severe winter.

9) Lamb production and Protostrongylus spp. levels were related to winter nutrition. Data were inadequate to compare horn and body growth between burned and unburned ranges.

10) Horn growth of yearling rams was greater on burned range than on unburned range but this early disparity was lost by the time rams were shot by hunters. Lamb production was higher and parasite levels were lower for sheep that wintered on burned range than for sheep wintering on alpine ridges, but this situation was an exception because most burned range is unavailable in winter due to deep snow.

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APPENDIX A. BIRDS AND MAMMALS SIGHTED IN THE TOAD RIVER AREA

Birds

Common loon
Horned grebe
Whistling swan
Canada goose
Mallard
Pintail
Green-winged teal
Cinnamon teal*
American widgeon
Shoveler
Scaup
Barrow's goldeneye
Bufflehead
Oldsquaw
Harlequin duck
Surf scoter
Ruddy duck
Common merganser
Goshawk
Sharp-shinned hawk
Red-tailed hawk
Golden eagle
Bald eagle
Harrier
Peregrine falcon
Kestrel
Blue grouse
Spruce grouse
Ruffed grouse
Willow ptarmigan
Sora
Killdeer
Greater yellowlegs
Lesser yellowlegs
Spotted sandpiper
Snipe
Herring gull
Great horned owl
Common nighthawk
Belted kingfisher
Flicker
Pileated woodpecker*
Yellow-bellied sapsucker
Hairy woodpecker
Northern three-toed woodpecker
Eastern kingbird*
Say's phoebe
Eastern phoebe
Least flycatcher
Traill's flycatcher
Horned lark
Tree swallow
Bank swallow
Barn swallow
Violet-green swallow
Cliff swallow
Gray jay
Raven
Black-capped chickadee
Boreal chickadee
Dipper
Robin
Varied thrush
Townsend's solitaire
Swainson's thrush
Hermit thrush
Mountain bluebird
Water pipit
Cedar waxwing
Bohemian waxwing
Northern shrike
Starling
Yellow warbler
Yellow-rumped warbler
Townsend's warbler
Wilson's warbler
Blackpoll warbler
Yellow-headed blackbird*
Rusty blackbird
Brown-headed cowbird
Gray-crowned rosy finch
Common redpoll
Hoary redpoll
Pine siskin
Savannah sparrow
Oregon junco
Tree sparrow
Chipping sparrow
Golden-crowned sparrow
White-crowned sparrow
Vesper sparrow
Song sparrow

Birds cont'd

Lapland longspur
Smith's longspur
Snow bunting

Mammals

Little brown bat
Snowshoe hare
Woodchuck
Hoary marmot
Red squirrel
Least chipmunk
Flying squirrel
Beaver
Deer mouse
Jumping mouse
Porcupine
Wolf
Coyote
Red fox
Black bear
Grizzly bear
Marten
Short-tailed weasel
Lynx
Cougar*
Mule deer
Elk
Moose
Caribou
Mountain goat
Stone's sheep

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* denotes species which are beyond their normally reported range.

APPENDIX B. BODY WEIGHTS AND MEASUREMENTS OF STONE'S SHEEP

Published data on body measurements of Stone's sheep are sparse. Cowan and Guiguet (1978) gave measurements for 4 rams and 1 ewe; Geist (1971) presented weights and measurements for 2 rams and 1 ewe. Geist (1971) and Banfield (1974) suggested that Stone's sheep were larger than Dall's sheep but noted that unequivocal evidence was lacking.

Weights and measures presented here are from sheep captured in the late June and early July at Churchill mineral lick. Also birth weights of 3 lambs at the Okanagan Game Farm are included. Comparisons are made to Dall's sheep and regressions between linear measurements and body weights are presented.

RESULTS AND DISCUSSION

The birth weights of captive, Stone's sheep lambs (3.3 ± 0.4 kg, $N = 4$) were similar to weights of newborn Dall's sheep in the wild (3-4 kg, Bunnell and Olsen 1976). In early July, when the wild Stone's lambs were between 4 and 6 weeks of age, their sizes and weight were extremely variable. This variation was not solely due to the small sample because many other lambs observed, but not captured, were comparable to extremes of size among the 3 captured lambs. Cause of the variation is not known (different ages or different growth rates), but it could result in smaller sized lambs failing to grow to an adequate size to survive the winter (Bunnell 1980).

Female yearlings were about 46% of the average weight of adult ewes. Male yearlings tended to be larger than female yearlings in all weights and measurements, but there was a great deal of overlap. Adult ewes were about 75% of the weight of the adult Stone's ram (77.3 kg) weighed by Geist (1971).

Bunnell and Olsen (1976) reported the following measurements for adult, Dall's sheep ewes ($\bar{x}$, range): weight (48.8 kg, 46.4-50.5), hind foot length (37.1 cm, 35-39), chest girth (108.5 cm, 105-112). Stone's sheep appear nearly identical in weight and size to Dall's sheep (Table 1). Because the Dall's sheep were weighed during winter or early spring and the Stone's sheep were weighed during summer, Dall's sheep may be marginally heavier (allowing for overwinter weight loss). However, hind foot lengths did not differ between the subspecies. The

Table 1. Body measurements of Stone's sheep.

	Weight (kg)	Hind foot length (cm)	Chest girth (cm)	Chest height (cm)	Shoulder height (cm)	Right horn length (cm)	Left horn length (cm)
Adult ewes							
$\bar{X}$ ± S.D.	49.6 ± 4.5	37.9 ± 1.3	95.6 ± 3.8	49.3 ± 3.7	88.3 ± 6.4	26.4 ± 5.8	25.3 ± 6.5
Range	44.5 - 55.8	35 - 40	87 - 101	40 - 54	70 - 95	17.5 - 38.0	17.0 - 39.0
n	6	15	15	15	15	15	15
Female yearlings							
$\bar{X}$ ± S.D.	22.7	35.9 ± 2.8	73	42.8 ± 2.1	73.5 ± 2.9	6.0 ± 2.9	5.3 ± 3.7
Range	19.1 - 26.3	33 - 39	73 - 73	41 - 45	70 - 77	2.0 - 9.0	1.0 - 10.0
n	2	4	2	4	4	4	4
Male yearlings							
$\bar{X}$ ± S.D.	27.7 ± 2.8	36.8 ± 1.7	76.3 ± 3.2	45.5 ± 1.0	76.3 ± 3.5	8.1 ± 2.8	8.4 ± 4.4
Range	24.5 - 30.4	35 - 39	73 - 79	45 - 47	72 - 80	4.0 - 10.0	2.0 - 11.2
n	4	4	4	4	4	4	4
Male lambs (July)							
$\bar{X}$ ± S.D.	11.5 ± 5.3	27.3 ± 3.8	52.5 ± 10.1	35.7 ± 4.9	55.7 ± 6.7	0	0
Range	5.4 - 15.4	23 - 30	41 - 60	30 - 39	48 - 60	-	-
n	3	3	3	3	3	3	3
Captive lamb birthweights							
$\bar{X}$ ± S.D.	3.3 ± 0.4	-	-	-	-	-	-
n	3						
Ovis dalli dalli adult ewes[a]							
$\bar{X}$	48.8	37.1	108.5				
Range	46.4 - 50.5	35 - 39	105 - 112				

[a] Bunnell and Olsen 1976

apparent difference in chest girth measurements was most likely due to a difference in measurement techniques between studies.

Regressions for Stone's sheep (Table 2) predicted body weight from linear measurements with confidence limits of less than ± 2.5 kg at the mean. Computed confidence limits were ± 1.5 kg, ± 1.8 kg, and ± 2.3 kg for chest girth, horn length, and hind foot length, respectively. The relationship between hind foot length and body weight was linear for Stone's lambs and yearlings, but there was no relationship between these measurements in adult ewes.

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Table 2. Relationships between body weight and measurements of Stone's sheep.

	Regression equation	r^2	Sy.x
Chest girth (G)	W = -37.5 + (0.88)G	0.96	3.15
Longest horn length (HL)	W = 18.7 + 1.13 HL	0.91	4.2
Hind foot length (HF) (for lambs and yearlings)	W = -32.8 + 1.64 HF	0.92	2.6

APPENDIX C. THE EFFECT OF BURNING AND FERTILIZATION ON STONE'S SHEEP RANGES

Subalpine grassland ranges are regularly burned during the spring in the Toad River area in an effort to prevent forest encroachment and to improve range quality. Also, some alpine areas have recently been fertilized by the Fish and Wildlife Branch to improve Stone's sheep range. I attempted to evaluate the value of these techniques by:

i) monitoring the effect of a subalpine grassland fire

ii) conducting alpine fertilization experiments.

Burning in alpine areas is not a viable technique because these areas are not able to carry a fire.

METHODS

SUBALPINE BURNING

The subalpine, grassland slopes of Fertilizer Mountain were burned by local residents in mid-May, 1981. I selected four unburned areas and four adjacent burned areas on the slopes and measured plant biomass in these areas by clipping 0.25 m^2 plots throughout the summer. Forage samples were collected for protein and proximate analysis. Soil samples were collected (top 10 cm of soil) from these areas and analyzed for nitrate, phosphorous, potassium, and sulphur.

ALPINE FERTILIZATION

Experiment 1

In 1980, two 0.25 ha plots in the alpine zone of Fertilizer Mountain were fertilized with 34% nitrogen fertilizer (17% nitrate, 17% ammonium) at a rate of 5 g/m^2 in early June, prior to new production. Plant biomass was measured on these areas and adjacent unfertilized areas in mid-August by clipping 0.25 m^2 plots. These areas were sampled again in 1981 and 1982. Forage samples were analyzed for protein and fibre in 1980 and 1981.

Experiment 2

In 1982, two 500 m^2 plots in the alpine zone of Tower Mountain were fertilized with 27-3-3 fertilizer (19.5% water soluble N, 6.8% water insoluble N) at a rate of 13 g/m^2. Plant biomass was measured by clipping 0.25 m^2 plots in early August. Forage samples were analyzed for protein and *in vitro* dry matter digestibility. Soil samples (top 10 cm) were collected and analyzed for total N, P, and K.

DISCUSSION

SUBALPINE BURNING

The spring fire initially set back the production of graminoids and forbs but by late June plant biomass was similar on burned and unburned plots (Table 1). At the end of the growing season there was no significant difference in the amount of graminoids and forbs on burned versus unburned plots. Forage quality (ADF and protein) was not significantly different between burned and unburned plots (Table 2). Similarly, soil mineral levels were not significantly different on burned versus unburned plots (Table 3).

Burning the winter carryover on these slopes in spring would volatilize about 0.6 g of nitrogen/m^2. The fires usually did not burn soil organic material. Very frequent burning may eventually deplete soil nitrogen levels unless the loss can be balanced by nitrogen-fixing legumes. As previously mentioned in the thesis (Table 11), Fertilizer Mountain soils tended to have higher phosphorous and potassium levels than soils from other areas in the vicinity which may be related to the frequent burning interval on this slope.

Overall, the effect of spring burning of subalpine ranges was not clearly beneficial or detrimental to range quality. However, it does maintain the areas as grassland by killing encroaching poplars. Caution should be exercised by not burning too frequently in order to prevent nitrogen depletion of the soils.

Even if burning did improve range quality, it would be impossible to improve critical areas of Stone's sheep winter range because the areas which were heavily grazed in winter (Fig. 4 in thesis) did not contain enough fuel in spring to carry a fire. These areas remained unburned

Table 1. Graminoid and forb production on burned versus unburned plots on Fertilizer Mountain following a spring burn ($\bar{X} \pm SE$, n=4).

	Graminoid Biomass (g/m^2)		Forb Biomass (g/m^2)	
	burned	unburned	burned	unburned
May 25	8.7 ± 1.5	18.9 ± 0.9	0.0	18.8 ± 0.8
June 17	37.7 ± 8.7	38.9 ± 6.8	20.1 ± 6.9	35.5 ± 11.5
July 4	62.8 ± 17.6	66.0 ± 10.0	52.0 ± 17.2	30.8 ± 6.0
July 26	58.4 ± 9.7	44.0 ± 5.9	20.0 ± 11.2	34.8 ± 8.0
August 12	55.5 ± 13.7	53.0 ± 9.9	16.0 ± 4.7	26.3 ± 7.9

Table 2. Protein and ADF levels in graminoids on burned versus unburned plots on Fertilizer Mountain following a spring burn ($\bar{X} \pm SE$).

	Crude Protein (%)				ADF (%)			
	burned	n	unburned	n	burned	n	unburned	n
May 25	21.6	2	19.9	2	23.9	2	29.3 ± 0.7	3
July 4	14.0 ± 1.9	4	13.5 ± 3.1	4	32.2 ± 1.5	4	30.1 ± 2.2	4
July 26	9.7 ± 1.1	4	7.9 ± 0.3	4	32.1 ± 0.9	4	33.4 ± 0.8	4

Table 3. Comparison of soil nutrient levels on burned versus unburned subalpine plots and fertilized versus unfertilized alpine plots ($\bar{X} \pm SE$).

	Total N %	nitrate %	P %	K %	S %	n
Subalpine						
burned	-	u	17.0 ± 2.5	370 ± 99.1	7.8 ± 0.64	4
unburned	-	u	16.1 ± 1.7	393 ± 78.0	7.1 ± 0.62	4
Alpine						
fertilized	0.65 ± 0.1	u	0.8 ± 0.5	70 ± 39.0	-	4
unfertilized	0.43 ± 0.1	u	u	70 ± 39.0	-	4

u = undetectible, less than 1.0 ppm.

whereas the dead carryover in the ungrazed areas was adequate to support the fire.

ALPINE FERTILIZATION

Fertilized plots did not produce significantly more graminoids or forbs than unfertilized plots in either experiment (Table 4). Forage quality was not significantly different between fertilized and unfertilized plots in either experiment although quality tended to be superior on fertilized plots in experiment 2 (Table 5).

In experiment 2, soil mineral levels were not significantly higher in the fertilized plots but nitrogen and phosphorous tended to be higher (Table 3). Although the data is inconclusive, it suggests that the level of fertilization in Experiment 2 was beginning to increase soil nutrient levels and forage quality but not forage production. This minor response was probably not adequate to be a significant benefit to the sheep using the range.

Table 4. Graminoid and forb production on fertilized and unfertilized alpine plots ($\bar{X} \pm SE$, n=5)

	Graminoid Biomass (g/m^2)		Forb Biomass (g/m^2)	
	fertilized	unfertilized	fertilized	unfertilized
Experiment 1				
August 1980, plot A	16.1 ± 1.8	21.4 ± 2.9	22.6 ± 3.7	18.7 ± 6.3
plot B	10.5 ± 3.4	16.2 ± 3.8	35.7 ± 7.6	39.8 ± 6.2
August 1981, plot A	8.4 ± 3.3	7.0 ± 3.6	23.1 ± 9.3	19.1 ± 4.8
plot B	6.9 ± 1.6	19.3 ± 2.6	26.2 ± 3.6	12.6 ± 5.1
August 1982, plot A	7.4 ± 3.9	5.1 ± 2.0	23.9 ± 7.6	22.2 ± 2.4
Experiment 2				
August 1982, plot A	5.4 ± 0.7	8.9 ± 3.1	24.7 ± 6.7	13.3 ± 4.6
plot B	6.1 ± 3.1	13.4 ± 2.4	53.4 ± 21.2	20.5 ± 5.9

Table 5. Forage quality of graminoids from fertilized and unfertilized alpine plots ($\bar{X} \pm SE$, n=4).

Date	Crude Protein (%)		ADF (%)		In vitro DMD (%)	
	fertilized	unfertilized	fertilized	unfertilized	fertilized	unfertilized
Experiment 1						
Aug 1980	10.0 ± 0.5	9.0 ± 0.4	26.8 ± 1.0	29.1 ± 1.2	-	-
Aug 1981	10.5 ± 0.9	11.4 ± 0.4	27.3 ± 1.3	25.2 ± 0.6	-	-
Experiment 2						
Aug 1982	11.1 ± 0.9	9.6 ± 0.2	-	-	60.8 ± 2.2	54.2 ± 3.7

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